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Handbook 654

Silvics of North America

Volume 1. Conifers

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Silvics of North America

Volume 1, Conifers

Russell M. Burns and Barbara H. Honkala
Technical Coordinators
Timber Management Research

Agriculture Handbook 654

(Supersedes Agriculture Handbook 271,
Silvics of Forest Trees of the United States, 1965)

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The silvical characteristics of about 200 forest tree species and varieties are described. Most are native to the 50 United States and Puerto Rico, but a few are introduced and naturalized. Information on habitat, life history, and genetics is given for 15 genera, 63 species, and 20 varieties of conifers and for 58 genera, 128 species, and 6 varieties of hardwoods. These represent most of the commercially important trees of the United States and Canada and some of those from Mexico and the Caribbean Islands, making this a reference for virtually all of North America. A special feature of this edition is the inclusion of 19 tropical and subtropical species. These additions are native and introduced trees of the southern border of the United States from Florida to Texas and California, and also from Hawaii and Puerto Rico.

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Foreword

"Silvics of Forest Trees of the United States," Agriculture Handbook 271, was the first comprehensive document of its kind in the United States. It was an edited compendium of research papers describing silvical characteristics of 127 trees; the papers had been independently prepared by specialists at U.S. Department of Agriculture Forest Service experiment stations. The original "silvics manual" took 10 years to complete and was published in 1965.

Our store of silvical and related knowledge has markedly increased since that silvics manual was published 25 years ago. The "Woody-Plant Seed Manual" of 1948 was updated in 1974 and issued as Agriculture Handbook 450, "Seeds of Woody Plants in the United States." New names were added to the literature in 1979 with Agriculture Handbook 541, "Checklist of United States Trees (Native and Naturalized)," which superseded Agriculture Handbook 41. In 1980, the 1954 Society of American Foresters' publication, "Forest Cover Types of the United States and Canada," was revised. A six-volume "Atlas of United States Trees" (U.S. Department of Agriculture Miscellaneous Publications 1146, 1293, 1314, 1342, 1361, and 1410) added tree range maps of most major and minor tree species to the literature. It was both appropriate and timely, therefore, to revise the information in the original silvics manual and to add other native and naturalized trees to the compendium.

"Silvics of North America" describes the silvical characteristics of about 200 conifers and hardwood trees in the conterminous United States, Alaska, Hawaii, and Puerto Rico. Individual articles were researched and written by knowledgeable Forest Service, university, and cooperating scientists. They were reviewed by their counterparts in research and academia. The project took 10 years to complete. The revised manual retains all of the essential material from the original publication, plus new information accumulated over the past quarter of a century. It promises to serve as a useful reference and teaching tool for researchers, educators, and practicing foresters both within the United States and abroad.

Jerry A. Sesco
Deputy Chief for Research

The use of trade names in this publication is for the information and convenience of the reader, and does not constitute official endorsement or approval by the U.S. Department of Agriculture of any product to the exclusion of others that may be suitable.

This publication also reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

Acknowledgments

This handbook is the result of a servicewide project of Timber Management Research, Forest Service, U.S. Department of Agriculture. It is an expansion of "Silvics of Forest Trees of the United States," originally published in 1965, and supersedes that handbook.

Individual papers contained in the two volumes of "Silvics of North America" were written by research foresters at U.S. Department of Agriculture Forest Service experiment stations and at several universities. Technical content was edited by Russell M. Burns, Silviculturist, and compilation and coordination of the project were by Russell M. Burns and Barbara H. Honkala, Botanist, of Timber Management Research, Washington, DC. Barbara Honkala revised the tree range maps and prepared lists of botanical, bird, and mammal names. Burns and Honkala prepared the glossary and the summary of shade tolerance classes, tree and flowering characteristics, type of seed germination, and order of soils on which trees most commonly grow. Robert L. Lyon, Entomologist, Arthur L. Schipper, and Charles S. Hodges, Jr., Pathologists, Forest Insect and Disease Research, Washington, DC, and Harold H. Burdsall, Jr., Mycologist, Process and Protection Research, Forest Products Laboratory, Madison, WI, reviewed and listed names of insects, mites, and organisms causing tree diseases. William G. Hauser, formerly of the Forest Service Permanent Image Collection, Washington, DC, assisted with the acquisition of photographs. Elbert L. Little, Jr., Dendrologist (retired), assisted in proofreading.

During the last year and a half, the project was directed by Robert D. Wray, Leader, Information Services (retired), North Central Forest Experiment Station. Wray edited the final revisions and guided the book through the production and printing processes. The North Central Station also provided clerical and administrative support during the pre-publication process. Robert P. Schultz, Assistant Director for Research, Southern Forest Experiment Station, served as technical reviewer and advisor for the final revisions.

The entire final proof was proofread under the direction of Mary Peterson and Barbara Winters, assisted by Gayla Conners, Sharon Fasthorse, Patricia Halter, Phyllis Moline, Rita Ronning, and Marcia Schardin, all of the North Central Forest Experiment Station. Personnel from the various Forest Service Experiment Stations carefully monitored the final revision and review of the chapters emanating from their Stations. Notable among these were: Margaret Buchanan, Northeastern Station; Louise Foley, Southeastern Station; Carlow Lowe and Jody Jones, Southern Station; Robert Hamre and Wayne Shepperd, Rocky Mountain Station; Richard Klade, Intermountain Station; Martha Brookes, Pacific Northwest Station; and Sandra Young, Pacific Southwest Station.

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The Tree and Its Environment

H. A. Fowells and Joseph E. Means

The mature forest tree is an outstanding example of interaction between the hereditary characteristics of an organism and its environment. The tiny embryo of the seed of the giant sequoia *(Sequoiadendron giganteum)* contains the potential to develop into the most majestic of plants. But if the environment is unfavorable, this potential will not be realized. Thus, responses of different species to environmental influences determine in part the success of silviculture. Silviculturists must know how the environment will affect the growth and development of trees they wish to manage.

Effects of environmental factors are generally the same for all trees. Reports in this publication describe known responses of each species to specific environmental conditions. This introduction provides background information of a general nature. The information offered here cannot approach the scope of texts on forest tree physiology, such as those by Kramer and Kozlowski and by Thimann (see General Notes and Selected References). Recently, Kozlowski *(26)* outlined specific effects of some environmental stresses on tree growth and development. More information on forest ecology is available in texts by Daubenmire and by Spurr.

The Total Environment

The total environment of a tree is a complex integration of physical and biological elements. The physical elements are related to climate and soil and include radiation, precipitation, and the movement and composition of air, as well as the texture of the soil and its structure, depth, moisture capacity, drainage, nutrient content, and topographic position. Biological elements are the plant associates; the larger animals that use the forest as a source of food and shelter; the many small animals, insects, and insectlike animals; the fungi to which the trees are hosts; and the microorganisms in the soil.

Complete and exact quantification of the environment is practically impossible. Some combinations of specific conditions have been used to characterize broad environmental regions and have been related to forest cover or vegetation type. Temperature indices were the basis for one classification system in which the climate of the United States was divided into seven temperature zones, each with its characteristic forest species, minor vegetation, and animal life *(39)*. In another system the North American continent was divided into six zones on the basis of the average temperatures of May, June, July, and August *(38)*. In a more complex scheme, winter temperatures, summer and winter dryness, and relative summer temperatures were considered *(24)*. Under this classification the southeastern United States is a single zone characterized by moderate or cool winters and moist warm summers.

A more widely used classification system is based upon precipitation effectiveness (P–E), a function of precipitation and evaporation, which represents the amount of precipitation available to plant growth *(69)*. Five climatic regions are recognized: superhumid, humid, subhumid, semiarid, and arid. These are associated with corresponding vegetation types: rain forest, forest, grassland, steppe, and desert. The subhumid region, or grassland, is divided into a moist subhumid and a dry subhumid. Some ecologists believe the moist subhumid region to be a forest region from which forests have been excluded by causes other than climate.

The superhumid region in North America includes the coastal forests of southern Alaska, Canada, Washington, Oregon, and northern California; the western slope of the Cascade Range in Oregon and Washington and of the Sierra Nevada in California; and also isolated areas in the Rocky Mountains, Appalachian Mountains, and New England. Western hemlock *(Tsuga heterophylla)*, Sitka spruce *(Picea sitchensis)*, coast redwood *(Sequoia sempervirens)*, western redcedar *(Thuja plicata)*, Douglas-fir *(Pseudotsuga menziesii)*, and grand fir *(Abies grandis)* are principal tree species in the western coastal part of the region. Western white pine *(Pinus monticola)*, ponderosa pine *(P. ponderosa)*, sugar pine *(P. lambertiana)*, and white fir *(Abies concolor)* are included with other species in mountain portions of the western part of the region. In the east, Fraser fir *(Abies fraseri)*, balsam fir *(A. balsamea)*, and red spruce *(Picea rubens)* are found in the superhumid region.

The humid region in the East includes most of the forest land, aside from the small areas of the super-

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The authors are H. A. Fowells, Chief, Branch of Silviculture, Timber Management Research (retired), USDA Forest Service, and Joseph E. Means, Research Forester, Pacific Northwest Research Station, Portland, OR. Fowells compiled the 1965 "Silvics of Forest Trees of the United States" and rewrote and updated the introduction for this revision. Means wrote the new section on "Potential Effects of Climate Change."

humid region described above. The humid region has been subdivided into four zones, with the oak–hickory type in the area with the lowest P–E index and the spruce–fir type in the area with the highest. In the West the broken topography of mountain ranges results in many discontinuities in the humid region. Here ponderosa pine, western larch (*Larix occidentalis*), Douglas-fir, incense-cedar (*Libocedrus decurrens*), and lodgepole pine (*Pinus contorta*) are typical species.

Within these broad provinces or regions, the interplay of local factors and general conditions often determines whether a species will be successful on a specific site. Thus, south-facing slopes tend to be warmer and drier than north-facing slopes, and low spots or openings in the forest may be frost pockets that restrict establishment of certain species. Soil drainage or depth is often decisive in limiting the presence or growth of trees in areas where climatic conditions are of near-critical importance.

Individual Environmental Factors

The impact of a change in environment can seldom be related directly to a single measurable factor in the total complex. Subtle interrelationships between environmental factors are usually present. Knowledge of how a plant responds generally to various individual factors is useful, however.

Temperature

Temperature directly affects the day-to-day physiological processes of plants and indirectly influences their seasonal or cyclic development. Plant processes, to the extent to which they are chemical reactions, tend to follow the van't Hoff law, namely, that the rate of reaction doubles for each temperature increase of 10° C (18° F). In such reactions the temperature coefficient is two.

In biological systems the law often operates only within narrow ranges, determined by the ability of the organism to survive. Thus, the temperature coefficient of respiration is two or more up to a temperature at which some essential respiratory enzyme is denatured. The process of photosynthesis has a temperature coefficient of less than two. Growth of cells has a temperature coefficient of about two, and even the overall growth of plants may show this response within the moderate temperature range. Because the temperature coefficient for photosynthesis is less than that for respiration, high temperatures may result in less photosynthate for growth.

For each plant there is a set of cardinal temperatures that controls its growth and development and, in fact, its existence: the minimum and maximum temperatures limiting growth and the optimum temperature for growth. For alpine plants the minimum temperature is close to 0° C (32° F), the maximum 20° to 30° C (68° to 86° F), and the optimum 10° C (50° F). For temperate plants the minimum temperature is about 4° C (40° F), the maximum 41° C (106° F), and the optimum 25° to 30° C (77° to 86° F). For tropical plants the minimum is 10° C (50° F), the maximum 50° C (122° F), and the optimum 30° to 35° C (86° to 95° F).

In a dormant or resting state, plants can endure extremes much greater than the minimum and maximum temperatures for growth. Evergreen trees endure winter temperatures of −51° to −57° C (−60° to −70° F), but temperatures of −4° to −1° C (25° to 30° F) kill twigs during the growing season. During summer in the temperate zones, temperatures may exceed 46° C (115° F), but growth is often completed before maximum temperatures occur.

Resistance to freezing temperatures, or frost hardiness, may result from a change in the protoplasm. The osmotic concentration of the cell sap increases with the hydrolysis of insoluble carbohydrates to soluble sugars (*13*). Dehydration of the protoplasm leads to an increase in the apparent bound water content of the proteins. Frost injury results from the formation of ice crystals within the protoplasm or the dehydration of the cell by ice formation in the intracellular spaces (*34*).

Heat resistance also appears related to a change in cellular proteins. The killing of cells by heat is brought about by denaturation of the proteins.

Thermoperiodicity

Plants not only respond to maximum, minimum, and optimum temperatures, but some also grow or develop best with an alternation of daily or seasonal temperatures. The growth of tomatoes was greatest when day temperatures were 27° C (80° F) and night temperatures were 17° to 20° C (63° to 68° F) (*73*). Similarly, loblolly pine (*Pinus taeda*) seedlings grew most with a day temperature of 27° C (80° F) and a night temperature of 17° C (63° F) (*27*). Several explanations have been offered for this phenomenon. The difference between the temperature coefficient of photosynthesis and that of respiration provides one explanation. Although photosynthesis increases with temperature, the rate of increase is not as great as that for respiration. Moreover, respiration continues 24 hours a day. When high day temperatures are followed by low night temperatures, therefore, more photosynthate remains for growth than when both day and night temperatures are high. Another explanation stems from an apparent decrease in translocation with increased temperature. Lower night temperatures would permit more rapid translocation of photosynthates from the leaves to meristematic tissue, favoring greater growth.

Some trees and shrubs fail to develop properly if they are not exposed to low temperatures during their dormant period. Thus, some deciduous fruit trees will not break dormancy if they are not subjected to near freezing temperatures for a minimum number of hours. Observations unsupported by controlled experiments suggest that some northern or subalpine conifers require a cold treatment to break dormancy and induce seasonal growth. It also has been demonstrated that certain nondeciduous shrubs, like camellia, show optimum blooming with cyclic temperatures *(7)*. Flower buds of camellia are initiated at temperatures of 24° to 27° C (75° to 80° F), but blooming is optimum at temperatures of 10° to 16° C (50° to 60° F).

Light

Visible light, that part of the electromagnetic spectrum with wavelengths in the range of about 400 to 760 millimicrons, plus ultraviolet and infrared light, affect the growth of trees in several distinct ways. The role of light as the source of energy for growth in photosynthesis is commonly known, but its role in regulating growth is more subtle.

Quality, intensity, and duration of light energy bear upon the photosynthetic process. Chlorophyll absorbs light more readily at wavelengths between 420 and 480 millimicrons and between 620 and 700 millimicrons. Light energy of these parts of the spectrum, corresponding to the blue-violet and the orange-red, is most efficient in the photosynthetic process. There is evidence that the color of foliage of various conifers and broadleaf trees results in differential responses to parts of the spectrum *(10)*.

Understory trees are probably exposed to light of quite different quality than overstory trees. Crowns of the overstory absorb part of the blue and red light and reflect or transmit green and yellow. Thus, light in the understory is relatively higher in green and yellow light.

Intensity of the light, or irradiance, measured in terms of energy per unit area per unit time, as gram-calories per square centimeter per minute, also affects the rate of photosynthesis. The irradiance on a clear summer day at sea level in the middle latitudes is about 1.5 g-cal per cm² per minute. This corresponds to an illumination value of about 10,000 foot-candles as commonly measured with a light meter.

Trees vary with respect to the light intensity at which maximum photosynthesis occurs. The rate of photosynthesis of loblolly pine increases with increasing light intensity up to full sunlight. The rate of photosynthesis of associated hardwoods, such as oaks *(Quercus)* and dogwood *(Cornus)*, however, does not increase at light intensities higher than about 30 percent of full sunlight *(28)*. Similarly, Engelmann spruce *(Picea engelmannii)* reaches near maximum photosynthesis at 4,000 to 5,000 foot-candles but lodgepole pine does not appear to be light saturated at 12,000 foot-candles *(55)*. For Japanese larch *(Larix leptolepis)*, the saturation point of light intensity is twice as high as that for white fir, Sitka spruce, or western hemlock. There is evidence that the metabolic pathway in larch may be different from that of nondeciduous conifers *(14)*.

Differences in photosynthesis among tree species are related to the arrangement of the leaves and resultant mutual shading; to the morphology of the leaves, as sun-leaves and shade-leaves; and perhaps to the chlorophyll concentration of leaves. One of the characteristics of trees termed "shade tolerant" is undoubtedly their ability to carry on photosynthesis at low levels of illumination. Seedlings of red alder *(Alnus rubra)*, a shade-intolerant tree, attain a higher rate of photosynthesis per unit of foliage weight than do seedlings of Douglas-fir, Sitka spruce, or western hemlock. Rates are similar per unit of foliage area, however. Also, the photosynthetic rate of red alder is much higher at light intensities greater than 3,100 foot-candles *(30)*.

The ability of tolerant trees to grow rapidly under low light intensities may be enhanced by the greater carbon dioxide concentration under a forest canopy. There is evidence that photosynthesis increases if the carbon dioxide concentration is more than the normal 330 parts per million found at sea level. Very high light intensities may in fact inhibit photosynthesis. Seedlings that normally develop under an overstory may not photosynthesize at a maximum rate if exposed to the full-light conditions of clearings or openings *(25)*.

There is conflicting evidence concerning efficiency in photosynthesis among provenances of various species. Genetic variation in photosynthetic efficiency was found in families of Douglas-fir seedlings; however, selection for that efficiency will be valuable only if seedling values are strongly correlated with mature growth *(9)*. Photosynthetic rates of Douglas-fir from western Oregon were higher than those from western Montana. Environmental conditions affected photosynthetic rates more than the seed source *(66)*. For jack pine *(Pinus banksiana)*, the rates of photosynthesis varied among provenances according to the time of year *(35)*. Differences in rates also were observed in Scotch pine (*Pinus sylvestris*) from Poland and from Turkey *(2)*. In Douglas-fir, rapid growth appeared to be related more to photosynthetic area than to efficiency of the foliage *(18)*.

The duration of illumination also affects the total amount of photosynthesis. Plants carry on photosynthesis continuously when exposed to light for 24 hours a day. However, the effect of the duration of illumination on photosynthesis and its resultant effect on growth probably is confounded with the temperature-regulating effect of day length on growth.

Light regulates growth and development of a tree through a number of incompletely understood reactions. One of these is the photoperiodic control of growth and flowering. Many tree species either cease terminal growth or continue to grow, depending on the duration of light within a day. A number of angiosperms and gymnosperms cease growth when exposed to only 8 hours of light a day *(11)*. Scotch pine, loblolly pine, and Virginia pine (*Pinus virginiana*) seedlings grow continuously on 14-hour days and with repeated flushes on 16-hour days. Some broad-leaved trees, such as red maple (*Acer rubrum*), birch (*Betula*), elm (*Ulmus*), and catalpa (*Catalpa*), grow continuously with exposure to 16-hour days, while others, such as sweetgum (*Liquidambar styraciflua*) and horsechestnut (*Aesculus hippocastanum*), do not.

Thus, the photoperiodic control of terminal growth of trees may be a limiting factor in the north-south movement of a species, even within its natural range. For example, under natural day length, loblolly pine from Maryland grew poorly in northern Florida compared to local loblolly pine, but it quadrupled its growth when the natural day length was extended with artificial light *(50)*. Similarly, cuttings of black cottonwood (*Populus trichocarpa*) from coastal Alaska, latitude 60° 37′ N., stopped growth about June 20 when planted near Boston (lat. 42° N.) but continued growing for 2 months more when day length was increased to match that of the source of the cuttings in Alaska *(49)*. Day length also influenced the time of bud set in western hemlock, which has a long north-south range. Because bud set precedes the onset of dormancy and cold hardiness, this species should not be moved far in a north-south direction *(31)*. Variation in height growth resulting from day length may limit the selection of provenances of white spruce (*Picea glauca*) *(53)*.

Day length, or photoperiod, also influences growth in diameter. Under long-day conditions trees produce large-diameter, thin-walled cells, resembling springwood. A change to short-day conditions results in the formation of small-diameter, thick-walled cells resembling summerwood. The transition is related to the production of growth-regulators during the period of terminal elongation *(32)*.

The transition from large-diameter cells to small-diameter cells with changing day length has been noted in a number of species, including red pine (*Pinus resinosa*) *(32)*, Monterey pine (*P. radiata*) *(19)*, Caribbean pine (*P. caribaea*) *(3)*, and European larch (*Larix decidua*) *(77)*. The content of inhibitors seems to be related to the production of thick-walled cells, whereas the content of promoters appears related to shoot growth. The amount of growth substances has been shown to be related to photoperiod *(77)*. One might speculate that the absence of definite growth rings in many tropical trees is related to a more or less constant day length.

Little evidence is available to show photoperiodic control of flowering in forest trees. Judging from the widespread occurrence of the phenomenon of photoperiodism in many plants, it is probable that such control does exist. However, flowers were borne on trees of 34 species of pine growing in California at a latitude of about 38° N., even though the trees represented pine sources ranging from latitude 15° N. to 70° N., with corresponding differences in day length *(42)*.

Unequal distribution of light may indirectly affect the form of trees. Greater development of the crown on the lighted side of the tree than on the shaded side results in asymmetrical growth of the bole. Regular spacing of trees to ensure better distribution of light thus tends to promote good form.

Light may also be a factor in epicormic sprouting. On many tree species, dormant buds on the bole are stimulated and sprouts develop after trees are exposed when surrounding trees are cut.

Moisture

Although the presence of one component of the environment is no more essential than that of another to the growth of trees, moisture is very often a limiting factor. Within the continental United States, excluding Alaska, annual precipitation to which forests are exposed varies from an average maximum of about 3550 mm (140 in) to an average minimum of about 380 mm (15 in). Rather large areas of forests, particularly ponderosa pine, grow with less than 500 mm (20 in) of annual precipitation. Silvicultural measures that make more of the total moisture available to the tree crop very likely increase growth.

Total precipitation is often used as a measure to relate productivity of forests to moisture, but it is not completely satisfactory. Moisture is available to trees primarily through the soil, although there is some evidence that they absorb atmospheric moisture under conditions of moisture stress *(65)*. The moisture-holding properties of the soil mantle are therefore of major importance.

Seasonal distribution of precipitation has a bearing upon the effectiveness of total precipitation. In forests of the Sierra Nevada in California, summer rains are rare. Nearly all the moisture available for trees is the amount held in the soil from winter and spring precipitation. In some parts of the country the highest precipitation occurs in the summer months. In much of the East, on the other hand, precipitation is rather evenly distributed throughout the year. The growth of loblolly, slash, shortleaf, and longleaf pines *(Pinus taeda, P. elliottii, P. echinata,* and *P. palustris)* has been shown to be differentially related to the amount and seasonal distribution of rainfall as well as to its retention in the soil *(59)*.

In addition to precipitation ordinarily measured as rain or snow, forests in some sections of the country obtain moisture from "fog-drip." Along the Pacific coast, the redwood forests in California and the Sitka spruce–hemlock–Douglas-fir forests of Oregon, Washington, and British Columbia undoubtedly benefit from the water condensed from fog dripping to the ground. However, fog-drip is only a part of the climatic environment of these fast-growing forests. The longer growing season, mild summer and winter temperatures, heavy precipitation, and high relative humidity (which lowers evapotranspiration rates), in addition to the fog-drip itself, certainly favor the exceptionally high forest productivity of this narrow belt along the coast.

Water available to trees is either that held temporarily in the soil mass against the force of gravity or that held between the soil particles by surface tension (capillary water). Gravitational water drains out of the soil mass following a rain. Capillary water is generally available except after rains or periods of melting snow. Water held at two other levels of energy, hygroscopic water and water of hydration in certain minerals, is not available to trees.

Water generally available to trees is held by energy forces that range from 0.1 to 15 atmospheres. The lower level approximates the field capacity of the soil, or the amount of water held against gravity. The upper level approximates the permanent wilting point, or the soil moisture level at which a plant is no longer able to obtain water fast enough to prevent wilting, from which it cannot recover unless water is added. Theoretically, plants cannot recover even when water is added if the permanent wilting point is exceeded.

The permanent wilting point is not well defined, however, for plants that have thickened rigid leaves, such as those of conifers and evergreen broadleaf trees and shrubs. There is evidence that such plants can live in a quiescent state and can extract water from the soil beyond the permanent wilting point as determined conventionally *(61)*. This enables the tree to survive temporary droughts that might cause the death of more succulent plants.

Water serves as a solvent for minerals, gases, and various organic compounds; it is a major part of the protoplasm of cells and is essential to certain metabolic processes. Most of the water taken up by a tree is transpired, however, and the benefit to a tree of such water use is not fully understood. In pine and hardwood forests in Arkansas, for example, 4.8 mm (0.19 in) of moisture was used per day from the upper 1.2 m (4 ft) of soil during the early part of summer *(79)*. The loss from the 1.8-m (6-ft) soil layer was estimated to be 6.4 mm (0.25 in) per day, or about 63 500 liters of water per hectare (6,800 gal/acre) per day.

The transpirational use of water may be of no immediately apparent benefit to a tree, but the conditions leading to transpiration are conducive to growth. The rate of photosynthesis is greater during periods of low moisture stress than when moisture stress forces the closing of the stomata. Transpiration thus may appear to be a necessary accompaniment to the availability of moisture for growth processes and the conditions promoting gas exchange and photosynthesis. There is evidence that moisture stress late in the growing season increases the cold hardiness of seedlings *(6)*.

Soil Condition

In addition to being a reservoir for moisture for trees, soil provides all the essential elements required in growth except those from the atmosphere, carbon from carbon dioxide, and some oxygen. Obviously, soil also provides the medium in which a tree is anchored. The many characteristics of soil, such as chemical composition, texture, structure, depth, and position, affect the growth of a tree to the extent to which they affect the supply of moisture and nutrients. A number of studies have shown strong correlations between productivity of site or growth of trees and various soil characteristics such as depth and position on the slope. The relationships are often indirect.

Generally, soil contains all the chemical elements essential to the growth of plants. Some elements may not be present in large enough quantity to sustain growth, however. For example, zinc, which is necessary in only minute amounts, was so deficient in western Australia that the growth of pines was inhibited *(64)*. In the United States, deficiencies of potassium, phosphorus, and nitrogen have been observed, and the application of fertilizers has resulted in increased growth, greater fruit production, and more desirable foliage color *(74)*. The effects of fertilization may continue for some time; increased growth of black spruce *(Picea mariana)* continued for 9 years after fertilization with major elements *(72)*.

The level of soil nutrients sufficient for optimum growth of most species is not known. Some guides to the adequacy of nutrient levels may be obtained from foliar analysis. Admittedly the technique has flaws, but a number of studies in the forest and in pot culture show that the optimum growth of pine occurs when adequate nutrient availability is reflected by the following foliar concentrations: nitrogen, 2 to 2.5 percent; phosphorus, 0.13 to 0.2 percent; potassium, 1 percent; calcium, 0.3 percent. In white and red spruce the transition zone from deficiency to sufficiency seems to begin at these foliar concentrations: for nitrogen, 1.3 percent; for phosphorus, 0.14 percent; for potassium, 0.30 percent; for magnesium, 0.06 percent; and for calcium, 0.10 percent *(68)*. Foliar concentrations of potassium and phosphorus were found to be correlated with growth characteristics of white fir, but no close relation was shown with most soil elements *(22)*.

In some soils the concentration of certain elements may be too high to support vigorous growth of trees. Soils derived from serpentine often contain so much magnesium that growth is poor, perhaps because the competition of the magnesium depresses calcium intake resulting in calcium deficiency.

The ability of a soil to supply water and nutrients is strongly related to its texture and structure as well as to its depth. Coarse-textured soils, the sands, are low in nutrient content and in water-holding capacity. Fine-textured soils, the clays, may be high in nutrient content and have high water-holding capacity. Aeration is impeded in heavy clays, particularly under wet conditions, so that metabolic processes requiring oxygen in the roots are inhibited.

In clay soils, percolation of water into the soil, and soil aeration, are favored by aggregated soil particles rather than by a plastic structure or cemented layers of hardpans. Silvicultural practices to prevent the destruction of organic matter and the compaction of soil can provide better conditions of soil moisture and aeration.

Air Movement

The movement of air is usually not an important environmental factor except under extreme conditions. It has a minor effect in that an increase in wind velocity results in greater evaporation and transpiration, taking water that might otherwise be used for growth. Prevailing winds from a given direction usually result in deformation of the crown of a tree and uneven development of its bole. Although the direct physical effects of wind in uprooting or breaking trees may be calamitous, adjustment of silvicultural practices to avoid such damage is not feasible. Where prevailing winds are known to be strong, however, windfirm trees can be favored and cutting patterns adjusted to minimize effects *(15)*.

Potential Effects of Climate Change

Climate (temperature, precipitation, and wind), and atmospheric chemistry (including carbon dioxide (CO_2) supply and air pollution) directly affect plant life. They also indirectly affect plants through their impact on soils and soil biota, pests and other pathogens, and other disturbances. Important changes in the Earth's climate due to increases in "greenhouse" gases are inevitable, according to most climatologists *(17,43,57,62)*. Simulation models suggest that the climate of the Earth is beginning to change at a rate unprecedented in the history of contemporary plant and animal species *(51,57)*. These changes would significantly affect reproduction, growth, and mortality of forest trees *(76)*. Thus, many of the data and relations described in this manual will be altered if climate and atmospheric chemistry change as projected.

How May Climate Change?

Mean annual global temperature is projected to rise 2° to 6° C (4° to 11° F) by the middle or end of the 21st century *(17,43,57,62)*. Most models predict the warming will be greater at higher latitudes, but there is less agreement on changes in the spatial and seasonal patterns of temperature and precipitation for areas the size of the United States *(57)*. Given the rapid rate of projected changes, plant adaptations in physiology and range will have to be made within one or two lifetimes of most tree species. This contrasts sharply with changes following the last ice age when similar temperature increases occurred over 7000 years, giving forests and trees many generations to adapt. Further, climate change will probably continue as people add more of the greenhouse gases to the atmosphere.

Natural Range

Species ranges are likely to be modified greatly if projected climate changes occur. Zabinski and Davis *(78)* projected drastic reductions in the natural ranges of eastern hemlock *(Tsuga canadensis)*, American beech *(Fagus grandifolia)*, yellow birch *(Betula alleghaniensis)*, and sugar maple *(Acer saccharum)* if CO_2 doubled as two different atmospheric general circulation models predicted. The reductions in present range varied from 20 to 70 percent, with similar expansions of potential natural range as range boundaries shifted northward hundreds of kilometers. For the western United States under a doubled-CO_2 climate, Leverenz and Lev *(33)* projected significant changes in range or importance of Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, ponderosa pine *(Pinus ponderosa)*, western larch *(Larix laricina)*, and Engelmann spruce *(Picea engelmannii)*.

Although the natural ranges of many species will likely shift northward and upslope, some populations may not be able to expand into newly suitable areas because of the limited speed of natural migration compared to the speed of climate change *(78)* and barriers to migration, such as lowlands with inhospitable climate and agricultural and urban areas *(51,52)*.

Though mature trees may survive for long periods *(8)*, a population must be able to complete its life cycle in the new environment to survive. Populations at risk of local extinction include those near mountain tops where suitable climate may move above the mountain tops or zones of suitable soil, and those in isolated reserves. Populations that will be at low risk include those able to reproduce in the changing climate at their current sites, those far enough down mountain slopes that suitable habitat will occur upslope within dispersal distances as climate warms, those able to disperse over large distances, and those assisted by people.

Soils

Another component of environmental change, atmospheric pollution, will continue to affect trees, in part through its effect on soils. Acid deposition, including nitrate and sulfate, may acidify soils and leach nutrient cations, thus decreasing soil fertility in the long term *(5,54)*. Acidification also increases soluble aluminum that can be directly toxic to trees *(21)* and interfere with calcium uptake, reducing cambial growth, sapwood cross-sectional area, and leaf area, in turn. This latter mechanism has been suggested as a cause of red spruce decline in the northeastern United States *(58)*.

Moderate amounts of pollutant nitrogen deposition may increase available soil nitrogen *(1,5)*. In contrast, excess soil nitrogen from atmospheric pollution in the northeastern United States may have several detrimental effects on plants in addition to those already mentioned *(1)*. It may cause a decrease in fine-root biomass and energy allocated to mycorrhizal associates, leading to decreased uptake of phosphorus and water *(1)*, and it may predispose conifer foliage to winter damage *(13)*.

Soil organic matter increases markedly (up to 3-fold) from grasslands through forests on mountain slopes *(20)*. This is controlled in part by decreasing temperature. If temperature increases as projected, decomposition of litter and soil organic matter will speed up. This may cause equilibrium organic matter content to decrease in the absence of compensating increases in productivity. If this occurs, the increased nitrogen released may temporarily but significantly increase forest growth. Soil organic matter and available soil nitrogen are projected to change ± 80 percent and ± 36 percent, respectively, in some northern forests under a doubled-CO_2 climate, depending on latitude and soil water-holding capacity *(48)*.

Damaging Agents

Growth and fuel accumulations may increase in the future on sites with equivalent droughtiness because increased CO_2 fertilization often increases net photosynthesis and decreases water use *(29,67)*. Death of established trees from stresses caused by environmental change would add to these fuels. Higher fuel loadings and warmer climate would probably increase wildfire intensity. Wildfire frequency for a region may also increase as climate warms (assuming the currently widespread relation between increased drought and increased fire frequency still holds) *(36)*, and precipitation does not increase.

Pest outbreaks may increase in forests where existing drought increases *(37)*. Fertilization by CO_2, however, may partially compensate for physiological stress caused by drought and higher temperature *(29)*. Forest pests, such as the balsam woolly aphid *(44)* and pine wilt disease *(56)*, that have ranges controlled by climate will probably have range shifts. Precipitation and temperature are known to influence population of some forest pests, for example southern pine beetle *(Dendroctonus frontalis)* *(40)* and gypsy moth *(Lymantria dispar)* *(4)*, so climate changes may significantly affect magnitude and frequency of pest outbreaks.

Changes in frequencies and intensities of other natural damaging agents (high-speed winds, temperature extremes, lightning, ice storms, and droughts) may also occur with climate change and thus adversely affect forest trees *(41)*.

Continued atmospheric pollution will compound some of these effects. For example, studies have shown that pollutants can reduce the growth of ponderosa pine and increase infection and mortality from bark beetles *(16)*.

Growth and Biomass Accumulation

Simulation experiments in eastern North America suggest that doubling or quadrupling CO_2 may increase biomass of natural northern stands by 70 percent or more (50 to 80 Mg/ha (30 to 45 ton/acre)) and decrease biomass of natural southern stands by 60 percent or more, depending on specific conditions *(48, 63)*. Factors not included in these simulations, such as the potential increased ability of trees to tolerate drought under increased CO_2, may lessen growth reductions in southern stands *(11,38)*.

Increased CO_2 has also been shown to increase nitrogen fixation in black alder *(Alnus glutinosa)* and black locust *(Robinia pseudoacacia) (45)* and mycorrhizal colonization in white oak *(Quercus alba) (47)*. Moreover, carbon dioxide fertilization increases the ability of seedlings of some species to tolerate drought *(29,67)* and nutrient deficiency *(46)*.

Competition

Competition among many species may change significantly as CO_2 changes. Under high light in a greenhouse experiment with 1-year-old saplings, red oak *(Quercus rubra)* grew as fast as yellow-poplar *(Liriodendron tulipifera)* under ambient CO_2, but grew faster than yellow-poplar under doubled CO_2. Similar differences occurred with other species *(75)*. Elevated CO_2 commonly increases water-use efficiency of seedlings *(29,46,67)* but species differences are common. Water-use efficiency of water-stressed sweetgum *(Liquidambar styraciflua)* seedlings was increased more by elevated CO_2 than was that of loblolly pine *(Pinus taeda) (71)*. Thus, growth of sweetgum was reduced less by water stress than was that of loblolly pine *(70)*. This may allow sweetgum under elevated CO_2 to compete more favorably against loblolly early in succession on drier Piedmont sites. However, it is not known how these differences in seedling responses will affect competitive interactions over the lifetimes of large trees in ecosystems.

Genetics

As climate changes in some locales—for example, as temperature increases in boreal forests in Canada *(63)*—existing individuals may become better adapted and stand productivity may increase. In other areas, such as near the hot or dry limits of a species' range, existing individuals may become less well adapted *(33)* and productivity may decline *(63)*. Species with broadly adapted genetic bases, such as loblolly pine, sweetgum, and Douglas-fir, may be better able to adapt to environmental change than other forest trees *(23)*. People managing large tree-breeding programs with narrowly defined breeding zones (e.g., *60)* may find selected trees are poorly adapted to their original zones. Such programs, however, will provide an extremely large pool of measured and structured genetic diversity, potentially helpful to managers in finding trees adapted to changed climate. Determining the locales where a genotype or species will do well may be difficult, because its optimum environment will shift over the landscape if climate continues to change over a rotation. Adaptation of species to changing climate may be approached, however, by tree-breeding and silviculture programs that seek to maintain high genetic diversity within stands *(23)*, produce more heterozygous trees, and attempt to select genotypes that will be adapted to future environments.

Most of the potential responses to environmental change presented here are projections based on incomplete current knowledge, not reliable predictions. However, many projections suggest important changes in the silvical characteristics of trees and the ways we must manage them. The speed of environmental changes may cause responses, such as wildfire, that produce major change in landscapes before noncatastrophic responses cause similar alterations in established forests. Also, some of the most significant responses to environmental change will likely be surprises. So, people using this manual would do well to keep abreast of new research on expected environmental changes and impacts on trees and forests. Such information will be essential to adapt management to environmental changes, and there will be many opportunities to do so.

Conclusion

This general statement of the responses of trees to environmental factors has provided a basis for consideration of the detailed and specific information about individual species presented in the papers that follow. Knowledge of species' responses to environmental influences can guide silvicultural practices and determine their success. Thus, in efforts to favor pine in the mixed conifer forests of the west slope of the Sierra Nevada in California, it was found that white fir seedlings were very sensitive to late spring frosts, which seldom hurt ponderosa pine *(12)*. Overstory trees or understory brush can protect the firs against frost. Complete clearing, as by patch cutting, removes the protection and creates conditions in which fir regeneration cannot compete successfully with pine regeneration. In another instance, high light intensities as found in clearings inhibited Engelmann spruce but not lodgepole pine *(55)*.

Although much has been learned about environmental responses of individual species, information for some species is still extremely sketchy. Progress toward more intensive silviculture depends on our ability to fill in the gaps in our knowledge of silvics. In the words of Aristotle, the search for truth is in one way hard and in another easy. For it is evident that no one can master it fully nor miss it wholly. Each adds a little to our knowledge of nature and from all the facts assembled there arises a certain grandeur.

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General Notes and Selected References

This edition of the "silvics manual" differs from the original in length, format, and the number of species included. A wider geographical area is covered and species with other than commercial timber value have been added. To keep the present work to a reasonable length, descriptions and illustrations of genera and many of the pre–1965 citations contained in the earlier edition were omitted.

The task of preparing so extensive a collection of individual papers was formidable, and many decisions were dictated by practical considerations. Although the individual papers follow the same general pattern, no attempt was made to achieve uniformity of length, scope, or approach. Many differences in treatment are related to the importance of the species and the amount of information available in the literature. The following notes on specific points should be helpful.

Varieties

The importance of a variety within a species differs. Some varieties, particularly those important to forestry, are addressed separately. Others are discussed within the species treatment, or are described under the heading "Genetics." The term subspecies used in some instances is synonymous with variety.

Species Names

Within the text, scientific names of trees and other plants, insects, and diseases are given without specification of author or synonyms; these are provided in lists at the end of each volume. Scientific names are generally those that were in effect when the original writing was done. Common names of birds and mammals are used in the text; scientific names are provided in a list. Every effort has been made to achieve accuracy and consistency in use of scientific names, but as common names differ widely, uniformity was not attempted. References used for all names are included in the list that follows these notes. Names of trees follow "Checklist of United States Trees"; other plant names were checked against the "National List of Scientific Plant Names"; and mammal names were taken from the "Checklist of Mammals of the United States and the U.S. Territories."

Measurements

Metric units are used in the text with English equivalents in parentheses. Neither unit is uniformly accurate throughout because referenced units may have been either metric or English and because of rounding of numbers. Conversions of board feet to cubic meters, in particular, should be viewed as estimates rather than true measurements because of assumptions made in the conversion process.

Selected References

The following lists contain works that provide background information on a variety of topics relating to silvics.

Dendrology

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Abies amabilis Dougl. ex Forbes Pacific Silver Fir

Pinaceae Pine family

Peggy D. Crawford and Chadwick Dearing Oliver

Pacific silver fir *(Abies amabilis)*, also known as silver fir and Cascades fir, has a gray trunk, a rigid, symmetrical crown, and lateral branches perpendicular to the stem. It contrasts strikingly with the more limber crowns, acute branch angles, and generally darker trunks of its common associates—Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, and mountain hemlock *(T. mertensiana)*. The species name, *amabilis*, means lovely.

Habitat

Native Range

Pacific silver fir (fig. 1) is found in southeastern Alaska, in coastal British Columbia and Vancouver Island, and along the western and upper eastern slopes of the Cascade Range in Washington and Oregon. It also grows throughout the Olympic Mountains and sporadically in the Coast Ranges of Washington and northern Oregon. Near Crater Lake, OR, Pacific silver fir disappears from the Cascade Range and then reappears at a few locations in the Klamath Mountains of northwestern California. The major portion of its range lies between latitudes 43° and 55° N. *(35)*.

Climate

Climate throughout the range of Pacific silver fir is distinctly maritime. Summers are cool, with mean daily temperatures of 13° to 16° C (55° to 61° F), and winter temperatures are seldom lower than -9° C (16° F) *(35)*. Mean number of frost-free days ranges from 40 near tree line to more than 250 at low elevations *(26)*. Length of growing season also differs from year to year at a given location. Mean annual precipitation varies greatly, ranging from 6650 mm (262 in) on the west coast of Vancouver Island to an extreme low of 965 mm (38 in) on the eastern side of Vancouver Island. Average annual precipitation in the Cascade Range is more than 1500 mm (59 in); winter snowpacks are as much as 7.6 m (25 ft) deep *(9)*. A summer dry season is characteristic of this region, but Pacific silver fir is dependent on adequate soil moisture during the growing season. It is most abundant on sites where summer drought is minimal, such as areas of heavy rainfall, seepage, or prolonged snowmelt.

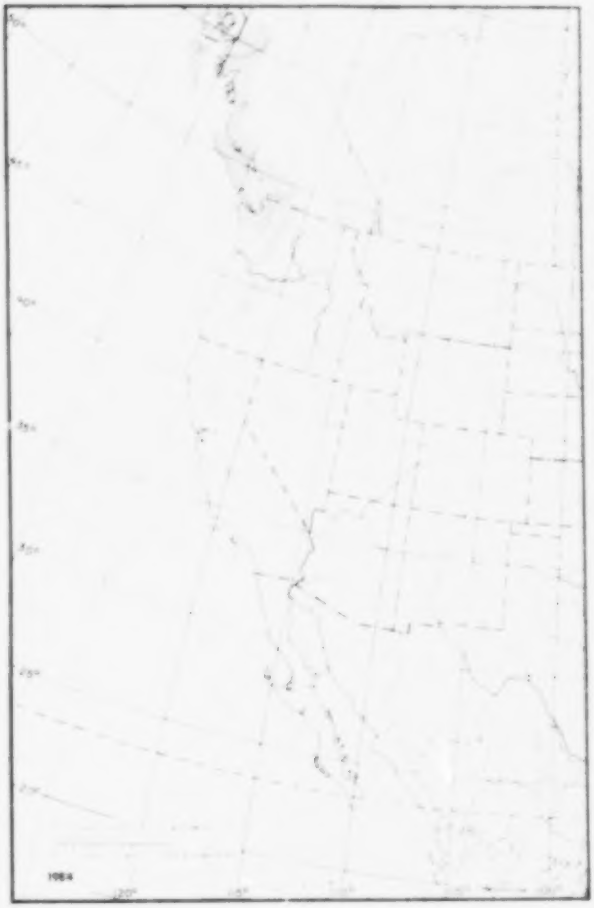

Figure 1—*The native range of Pacific silver fir*

Soils and Topography

Pacific silver fir grows on soils developed from nearly every type of parent material found in the Northwest. Layering in soil profiles caused by successive deposits of volcanic ejecta, colluvium, or glacial till is especially common *(1,43)*. The greatest known growth rates for Pacific silver fir occur at low elevations on fine-textured residual soils from

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sedimentary and basaltic rocks *(16)*. Growth is reduced on poorly drained or shallow rocky soils.

In northern Washington and British Columbia, podzolization is the dominant process in well-drained soils under Pacific silver fir. A typical podzol is characterized by strong acidity of organic (pH 3.3 to 4.0) and mineral horizons, moderate to thick (3 to 45 cm; 1 to 18 in) surface accumulations of organic matter, and moderate to extremely low base saturation. In Oregon, podzolization is less strongly expressed and soils are more shallow and rocky. Pacific silver fir has been found on many soil suborders throughout its range: Folists in the order Histosols; Aquents, Fluvents, Orthents in the order Entisols; Andepts, Aquepts, Ochrepts, Umbrepts in the order Inceptisols; and Aquods, Humods, and Orthods in the order Spodosols *(35)*.

At upper elevations in Washington, soils beneath Pacific silver fir stands are generally low in available nitrogen, with availability decreasing with age *(44)*. External nutrient cycling is slow; a mean nitrogen residence time as long as 120 years has been found in old-growth forest floors *(24)*. Nitrification has not been found to occur. Availability of phosphorus tends to be low but availability of base elements does not appear to limit plant growth *(42)*. Internal cycling meets much of the annual nutrient requirements. Foliar nitrogen concentrations between 0.7 and 1.2 percent and foliar phosphorus concentrations of 0.11 to 0.20 percent have been reported *(3,42,52)*. Pacific silver fir differs significantly from western hemlock in its ability to accumulate specific elements *(46)*.

Pacific silver fir grows at sea level along the coast from Alaska to the Olympic Peninsula; farther inland, it is absent at lower elevations. Its range in elevation is narrowest in Alaska, 0 to 300 m (0 to 1,000 ft), and greatest in the western Cascade Range of Washington, where Pacific silver fir may be found from 240 to 1830 m (800 to 6,000 ft). In British Columbia it is found from 0 to 1525 m (0 to 5,000 ft) in elevation on western Vancouver Island and from 180 to more than 1680 m (600 to more than 5,500 ft) on the lower mainland. Pacific silver fir grows on the highest ridges and peaks in the Coast Ranges of Washington, from 365 to 850 m (1,200 to 2,800 ft). In the Olympic Mountains, it is the predominant montane species up to 1400 m (4,600 ft), with lower limits at sea level on the west side and at 360 m (1,200 ft) in the central mountains. It is found between 610 and 1830 m (2,000 and 6,000 ft) in the Cascade Range in Oregon as far south as the divide between the Rogue and Umpqua Rivers. On the east side of the Cascade Range, it is confined to high elevations, down to 1160 m (3,800 ft) in Oregon and 1000 m (3,300 ft) in Washington *(30,35)*.

Associated Forest Cover

Western hemlock is a common associate throughout most of the range of Pacific silver fir, in the *Abies amabilis* zone and portions of the *Tsuga heterophylla* zone *(9)*. Noble fir *(Abies procera)* is an important associate in southern Washington and northern Oregon. Other associates west of the Cascade Range are Douglas-fir, western redcedar *(Thuja plicata)*, and grand fir *(Abies grandis)*, with Sitka spruce *(Picea sitchensis)* and lodgepole pine *(Pinus contorta)* important near the coast. At subalpine elevations in the *Tsuga mertensiana* zone *(9)*, Pacific silver fir is associated with mountain hemlock, Alaska-cedar *(Chamaecyparis nootkatensis)*, and subalpine fir *(Abies lasiocarpa)*. Toward the eastern limits of its range, it grows with a mixture of coastal and interior species: western larch *(Larix occidentalis)*, western white pine *(Pinus monticola)*, lodgepole pine, subalpine fir, grand fir, and Engelmann spruce *(Picea engelmannii)*. Shasta red fir *(Abies magnifica* var. *shastensis)* is an associate in the extreme southern portion of its range. Extensive pure stands of Pacific silver fir have been reported in the Mount Baker and Mount Rainier regions and elsewhere in the southern Washington Cascade Range *(40)*.

Pacific silver fir is a major species in the forest cover type Coastal True Fir–Hemlock (Society of American Foresters Type 226) *(5)*. It is also found in the following types:

205	Mountain Hemlock
206	Engelmann Spruce–Subalpine Fir
223	Sitka Spruce
224	Western Hemlock
225	Western Hemlock–Sitka Spruce
227	Western Redcedar–Western Hemlock
228	Western Redcedar
229	Pacific Douglas-Fir
230	Douglas-Fir–Western Hemlock

Shrubs associated with Pacific silver fir are primarily ericaceous. Blueleaf huckleberry *(Vaccinium deliciosum)*, Cascades azalea *(Rhododendron albiflorum)*, and rustyleaf menziesia *(Menziesia ferruginea)* are common understory species at higher elevations; copper bush *(Cladothamnus pyrolaeflorus)* is important in subalpine British Columbia *(2)*. Alaska huckleberry *(Vaccinium alaskaense)*, big huckleberry *(V. membranaceum)*, ovalleaf huckleberry *(V. ovalifolium)*, and devilsclub *(Oplopanax horridum)* are widespread associates. At its lower limits of elevation, Pacific silver fir is found with salal *(Gaultheria shallon)* and Oregongrape *(Berberis nervosa)*.

Common herbaceous associates are common beargrass (*Xerophyllum tenax*), bunchberry (*Cornus canadensis*), twinflower (*Linnaea borealis*), queenscup (*Clintonia uniflora*), dwarf blackberry (*Rubus lasiococcus*), strawberryleaf blackberry (*R. pedatus*), rosy twistedstalk (*Streptopus roseus*), coolwort foamflower (*Tiarella unifoliata*), and deerfern (*Blechnum spicant*). *Rhytidiopis robusta* is a constant bryophyte associate.

Major habitat types include *Abies amabilis–Tsuga mertensiana/Vaccinium membranaceum–Rhododendron albiflorum* on cold, wet sites at high elevations and *Abies amabilis/Xerophyllum tenax* on shallow coarse-textured soils at various elevations. *Abies amabilis/Vaccinium alaskaense* is a widespread type on modal sites. *Abies amabilis/Rubus lasiococcus*, *Abies amabilis/Streptopus roseus*, *Abies amabilis/Tiarella unifoliata*, and *Tsuga heterophylla–Abies amabilis/Blechnum spicant* are herb-dominated types found in moist habitats. The *Abies amabilis/Oplopanax horridum* type occupies wet, alluvial habitats *(2,9)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pacific silver fir is monoecious; self-fertilization is possible because times of pollen dispersal and seed cone receptivity overlap on the same tree. Flowers differentiate from axillary buds of current-year lateral shoots in early July of the year before seed development *(32)*. When receptive to pollination, the seed cones appear purple, erect, and 8 to 16 cm (3 to 6 in) tall on the upper surfaces of 1-year-old branches in the upper parts of tree crowns. Just before pollination, the pollen cones appear red, pendent, and usually abundant on the lower surfaces of the branches somewhat lower on the crowns than the seed cones. Cone buds burst the following May, and pollination occurs about 2 weeks later—before vegetative bud burst. The pollen does not germinate and begin forming its pollen tube until 4 to 5 weeks later, resulting in a 6-week delay between pollination and fertilization *(7,33)*.

Initiation of phenological events varies with latitude, altitude, aspect, weather, and snowpack and is apparently related to mean soil and air temperatures. For example, pollination may occur in mid-May at 900 m (2,960 ft) in central Washington but is delayed until mid-June at 1600 m (5,250 ft) and until late May in southern British Columbia *(7,32,33)*.

Seeds are fully mature in late August, and dissemination begins in mid-September—one of the earliest dispersal times for Pacific Northwest conifers. Initiation of dispersal is apparently independent of altitude or latitude *(7)*; most seeds are shed by the end of October but may be shed until the following April *(21,33)*.

Seed Production and Dissemination—Cone production begins at years 20 to 30 *(33,37)*. Good seed years vary from region to region; a good seed crop generally occurs every 3 years *(8)*. Pacific silver fir is not considered a good seed producer; this condition is attributed to frequent years of low pollen, the extended period between pollination and fertilization, and archegonial abortion producing empty seeds *(33)*. Percentage of sound seed varies, with reports of 6.7 to 35 percent and 51 percent in one location *(4)*. Germinative capacity varies widely—from 3 to 70 percent— but averages 20 to 30 percent. Cleaned seeds range from 17,200 to 45,860/kg (7,800 to 20,800/lb) *(37)*.

The seeds are heavier than seeds of most Pacific Northwest conifers except noble fir. Seeds each contain a single wing but often fall from the upright cone axis by pairs on ovuliferous scales, as the bracts contort and tear themselves from the cone—a process that does not require wind. When the seeds are dispersed by the wind, they do not carry far; unsound seeds are carried farther than sound seeds. In one study, only 9 percent of the sound seeds were found more than 114 m (375 ft) from the stand edge, compared with 41 percent at the stand edge and 34 percent more than 38 m (125 ft) *(4)*.

Seedling Development—Pacific silver fir germinates in the spring after overwintering under snow. Germination is epigeal *(37)*. Seedlings germinating on snow because of early snowfall or late seed fall are generally short lived. Germination can occur on a variety of media: on litter humps and in moist depressions in the subalpine zone; on edges of melting snowpack in subalpine meadows; and in litter, rotten wood, moss, organic soils, mineral soils, and fresh volcanic tephra *(2,11,25)*. Survival is better on mineral seedbeds than on organic seedbeds. Early mortality of seedlings is attributable more to germination on snow, adverse climatic effects, and competing vegetation than to disease *(18)*.

Cool, moist habitats are best for germination, but full sunlight produces maximum subsequent growth. Seedlings can also grow under dense shade; seedlings 8 to 12 years old and about 10 cm (4 in) tall can frequently be found beneath older, closed forest canopies. Seedlings that survive continue to grow very slowly, existing as advance regeneration that can be 65 to 110 years old and only 45 to 200 cm tall (18 to 80 in). When existing as advance regeneration, Pacific silver fir has flat-topped crowns caused by slow height growth relative to lateral branch growth.

Seedlings are sturdy and erect and resist being flattened by litter and heavy, wet snow. Survival of Pacific silver fir as advance regeneration at middle elevations, where western hemlock is primarily found in openings, is attributed partly to its ability to resist being buried by litter after snowmelt *(40)*. At the highest elevations, Pacific silver fir is found primarily in openings and less frequently beneath the canopy *(38)*. Stems of seedlings growing on slopes often have a "pistol-butted" sweep, caused by heavy snow creeping downhill.

Vegetative Reproduction—Although Pacific silver fir can produce epicormic or adventitious sprouts, it does not regenerate by stump sprouting. Upturning of lower branches after tops of young trees are cut may resemble sprouting.

Sapling and Pole Stages to Maturity

Growth and Yield—There is a broad range of height growth rates of Pacific silver fir because of the wide variation of climates with elevation and latitude. Site index values (at 100 years) in southern British Columbia range from 12 to 46 m (40 to 150 ft) *(26)* and have been negatively correlated with elevation in Washington *(16)*. In subalpine tree clumps at higher elevations, Pacific silver firs reach heights of 18 to 24 m (60 to 80 ft).

The largest Pacific silver fir tree known was in the Olympic National Park, WA. It was 256 cm (101 in) in d.b.h. and 74.7 m (245 ft) tall. Trees 55 to 61 m (180 to 200 ft) tall and more than 60 cm (24 in) in d.b.h. are common in old-growth stands. Trees 500 to 550 years old have been found on Vancouver Island and in the North Cascades National Park, WA. Maximum age reported is 590 years *(48)*.

Early height growth from seeds is generally considered very slow; 9 or more years are usually required to reach breast height. Juvenile height growth ranges from 10 to 40 cm (4 to 16 in) per year, depending on length of the growing season *(50)*. Planted seedlings also grow slowly, with height increments of 3 to 15 cm (1 to 6 in) for the first few years after planting *(47)*. On productive sites at low elevations, Pacific silver fir is capable of much greater rates, averaging 90 cm (35 in) per year above breast height on some 30-year-old trees *(16)*. Growth of released advance regeneration is more rapid than early growth from seeds *(20,49)*. After an initial lag following overstory removal (as by avalanche, windstorm, or clearcutting), growth rates of 50 cm (20 in) or more per year can occur *(49)*. When released from suppression, advance regeneration trees change from flat-topped to more conical crowns (fig. 2) *(41)*.

Table 1—Volume yield of second-growth stands in Washington and British Columbia, dominated by Pacific silver fir, based on sample plot data

Plot location and elevation	Proportion of Pacific silver fir[1]	Age	Density	Volume
	pct	*yr*	*trees/ha*	*m³/ha*
Washington:				
King County, 975 m	100	47	1,850	980
Whatcom County, 760 m	95	70	2,879	875
Vancouver Island, BC *(28)*:				
Santa Maria Lake, 533 m	85	100	1,361	1593
Labor Day Lake, 922 m	65	125	1,016	1505
Haley Lake, 1204 m	64	108	1,011	950
Haley Lake, 1119 m	59	92	1,302	1197
Sarah Lake, 116 m	53	111	420	1220
	pct	*yr*	*trees/acre*	*ft³/acre*
Washington:				
King County, 3,200 ft	100	47	749	14,004
Whatcom County, 2,500 ft	95	70	1,165	12,504
Vancouver Island, BC *(28)*:				
Santa Maria Lake, 1,750 ft	85	100	551	22,764
Labor Day Lake, 3,025 ft	65	125	411	21,506
Haley Lake, 3,950 ft	64	108	409	13,576
Haley Lake, 3,670 ft	59	92	527	17,105
Sarah Lake, 380 ft	53	111	170	17,434

[1] Based upon the total number of trees in sample plots.

Pacific silver fir occasionally shows an abnormal height growth pattern, in which various sapling and pole-size trees curtail height growth for at least 1 year while adjacent trees grow normally. Causes of this phenomenon are not known.

Height-age and site index curves for Pacific silver fir have recently been constructed *(23)*; however, little information on yield of second-growth stands is available. Data from sample plots on a variety of sites (table 1) indicate that large volumes can be expected from Pacific silver fir in pure stands or mixed with hemlocks. Close spacing and lack of taper are partly responsible for high volumes found in pure, even-aged stands of Pacific silver fir.

Volume in old-growth stands is extremely variable, depending on the mix of species and degree of stand deterioration. One densely stocked plot at 1100 m (3,600 ft) in the north Cascades had 1813 m³/ha (25,895 ft³/acre), 83 percent Pacific silver fir by volume. An older, more open stand in the same area had 840 m³/ha (12,000 ft³/acre).

Stands at upper elevations (predominantly Pacific silver fir) in western Washington carry large amounts of leaf biomass—18 to 25 t/ha (8 to 11 tons/acre); total standing biomass ranges up to 500 t/ha (223 tons/acre) in mature and older forests. Leaf area indexes of 14 have been reported *(14)*. A large proportion of the net primary production is below ground in subalpine stands; this is apparently a characteristic of the cool sites and low nutrient mobilization rates rather than the species itself. Values of net primary production in two upper elevation Pacific silver fir stands in western Washington were determined *(15)*. In the 23-year-old stand, total net primary production was 18 000 kg/ha (16,060 lb/acre); in the 180-year-old stand it was 17 000 kg/ha (15,170 lb/acre). Of this, the above-ground portion was 6500 kg/ha (5,800 lb/acre) and 4500 kg/ha (4,010 lb/acre) for the two stands, respectively. Woody growth made up 65 percent of this amount in the younger stand, and 50 percent in the older stand. The below-ground portion was 11 500 kg/ha (10,260 lb/acre) and 12 500 kg/ha (11,150 lb/acre) for the two stands, respectively. Small conifer roots and mycorrhizae made up 65 percent of this amount in the younger stand and 73 percent in the older stand.

Rooting Habit—Pacific silver fir seedlings have roots that more closely resemble a true taproot system than do western hemlock seedlings *(38)*, and the roots can penetrate more compact soils than can the roots of western redcedar, Sitka spruce, and western hemlock *(27)*. Seedlings can develop adventitious roots where volcanic tephra covers the original soil surface *(1)*. Advance regeneration has small root-to-shoot ratios, and the roots are predominantly in the organic layers. Mature Pacific silver fir can have a relatively flat, shallow, platelike root system on poorly drained or shallow soils or in areas where there is nutrient immobilization in the forest floor *(15)*. On soils where podzolization develops and organic matter accumulates, feeding roots become concentrated in organic horizons as a stand ages.

Peak growth of seedling roots occurs when shoots are least active. Activity is high in early spring and late autumn even in cold soils. Roots can also be active during the winter when soil temperatures are just above freezing; however, water conductance is dramatically reduced after seedlings are preconditioned to cold temperatures *(39)*. At upper elevations in both young and mature stands, a large proportion of annual biomass production is in the root systems *(15)*. Roots are intensely mycorrhizal at upper elevations, and *Cenococcum graniforme* is a major mycorrhizal symbiont *(45)*.

Reaction to Competition—Pacific silver fir can grow in a variety of stand development conditions. It can seed onto outwash after glacial retreat *(35)*, seed into burned areas, develop from advance regeneration after removal of the overstory, and grow slowly from a suppressed tree into an overstory tree in more uneven-aged stands where disturbances are minor.

Advance regeneration may have a cone-shaped crown or can become flat topped, with lateral branch growth greatly exceeding height growth. After extensive removal of the overstory, some (but not all) advance regeneration can accelerate in diameter and height growth and form a new forest *(20)* (fig. 2).

Even-aged, pure, or mixed stands vary in stocking but can have more than 2,470 stems per hectare (1,000/acre). When crowns close during the sapling and pole stages, understory vegetation is almost completely eliminated by shade, causing an open forest floor. Lower limbs become shaded and die, creating branchfree boles. This condition may last 200 years *(31)*.

Eventually the overstory crowns abrade and let more light into the understory, allowing development of shrubs and advance regeneration. This may occur after one to three centuries—probably depending on site quality, spacing, and disturbance history—and has been observed to last to age 500 years *(31)*. Individual overstory trees eventually die and advance regeneration grows slowly upward, creating a multi-

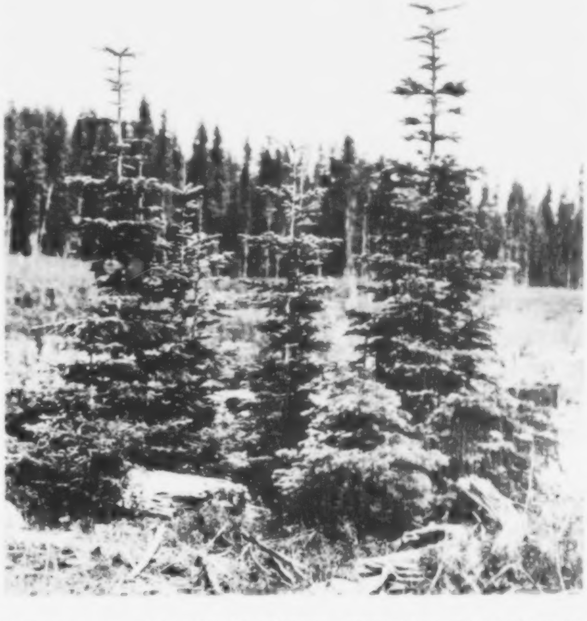

Figure 2—*Pacific silver fir advance regeneration after release by clearcutting.*

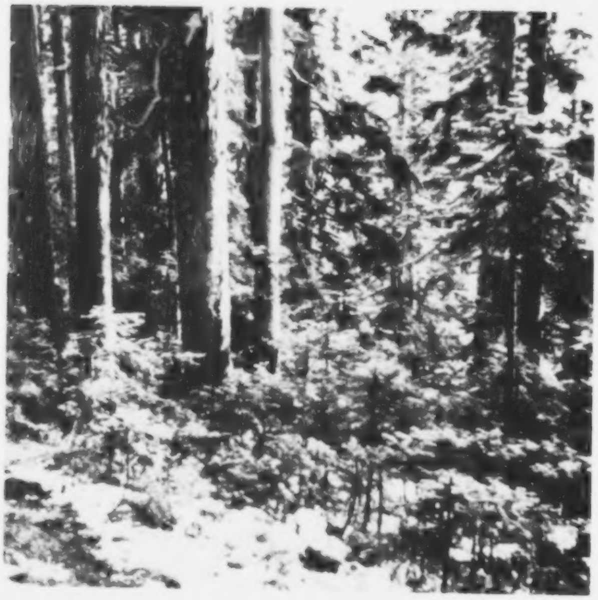

Figure 3—*Old-growth stand of Pacific silver fir. Barring a major disturbance, the overstory slowly breaks up and the tolerant Pacific silver fir grows in the partial shade. (Courtesy of Robert G. Wagner, Oregon State University, Corvallis)*

aged, old-growth forest with a major component of Pacific silver fir that will be self-perpetuating, barring a major disturbance (fig. 3). Pacific silver fir is referred to as the climax species at mid-elevations of its range *(9)* because of its ability to survive in the shade and to emerge in all-aged stands.

Because of its slow early height growth, associated species such as western hemlock, Douglas-fir, and noble fir initially overtop Pacific silver fir when grown in the open. After the initial overtopping, on many sites Pacific silver fir appears to outgrow and become taller than western hemlock after 100 years *(19)*. On cool, moist sites at the upper extremes of the range of Douglas-fir, Pacific silver fir can stratify above Douglas-fir as well *(40)*. Noble fir appears to maintain a height advantage over Pacific silver fir indefinitely on all sites where both species grow.

Pacific silver fir is one of the most shade-tolerant trees in the Northwest. There is confusion regarding its relative shade tolerance compared with western hemlock. It has been described as equal, greater, and less shade tolerant than hemlock *(26,40)*. It can most accurately be classed as very tolerant of shade.

Most silvicultural treatments of Pacific silver fir have dealt with regeneration and early stocking levels after old-growth stands were logged. Regeneration practices vary from clearcutting followed by burning and planting to clearcutting with reliance on natural advance and postlogging regeneration. Each practice successfully obtains regeneration for certain sites and management regimes. Early stocking control—thinning sapling and pole-size trees to 495 to 740/ha (200 to 300/acre)—is practiced to increase growth rates of individual trees. Trees left in pole-size stands after thinning markedly increase in diameter growth and apparently respond to fertilization. Possible commercial thinning regimes, rotation ages, and regeneration plans for managed stands (where advance regeneration may not be prevalent) are primarily in the planning stages.

Young, post-harvest stands can develop densely from advance regeneration. These stands may require thinning to maintain diameter growth, to keep from buckling in heavy snow or wind, and to ensure advance regeneration before the next harvest.

Damaging Agents—Pacific silver fir is easily killed by fire because of its shallow rooting habit and thin bark. It has lower resistance to windthrow than Douglas-fir, western hemlock, or western redcedar. It is susceptible to windthrow after heavy partial cuts *(9)*, on the borders of clearcuts or partial cuts, and even in closed canopy stands during strong winds. Resistance to breakage from snow and damage by frost is moderate. The foliage of *Abies amabilis* and other true firs is more easily damaged by volcanic tephra than is the foliage of associated conifers *(22)*. Several types of animal damage have been reported: heavy browsing by Roosevelt elk *(34)*, bark stripping by bears in pole-size stands, clipping of terminal buds by grouse and rodents *(13)*, and cutting of cones and cone buds by squirrels.

Pacific silver fir is susceptible to many types of insect damage. Seed chalcids *(Megastigmus pinus* and *M. lasiocarpae)* and cone maggots *(Earomyia abietum)* have been known to infest a high proportion of cones during good seed years *(17)*. Western hemlock looper *(Lambdina fiscellaria lugubrosa)* and western blackheaded budworm *(Acleris gloverana)* are serious defoliators of mixed Pacific silver fir and western hemlock stands in British Columbia. Many other loopers are of minor importance; two species that cause periodic outbreaks are the greenstriped forest looper *(Melanolophia imitata)* and saddleback looper *(Ectropis crepuscularia)*. The western spruce budworm *(Choristoneura occidentalis)* also feeds on Pacific silver fir in pure and mixed stands.

The silver fir beetle *(Pseudohylesinus sericeus)* and fir root bark beetle *(P. granulatus)* can be very destructive together and in combination with the root rotting fungi *Armillaria mellea*, *Heterobasidion annosum*, *Phellinus weiri*, and *Poria subacida*. The last major outbreak of silver fir beetles lasted from 1947 to 1955; it killed 2.5 million m^3 (88 million ft^3) of timber in Washington *(12)*.

An imported pest, the balsam woolly adelgid *(Adelges piceae)*, is the most devasting killer of Pacific silver fir. Attacks on the crown by this insect result in swelling or "gouting" of branch nodes, loss of needles, and reduced growth for many years; attacks on the stem usually cause a tree to die within 3 years. Trees of all ages and vigor are susceptible, although some individuals seem to have natural resistance. In southern Washington, damage has been heavy on high-quality sites at low elevations, such as benches and valley bottoms *(28)*. In British Columbia, heaviest damage is on similar sites below 610 m (2,000 ft). Pacific silver firs growing with subalpine firs at high elevations are relatively immune and suffer only temporary gouting. Spread of the aphid has been slow since the major outbreak of 1950–57, but infested areas remain a problem. No effective direct control methods have been found for forest stands.

Pacific silver fir is a secondary host for hemlock dwarf mistletoe *(Arceuthobium tsugense)* and can be infected in mixed stands containing western or mountain hemlock. *A. abietinum* also attacks Pacific silver fir and western hemlock; it is more common in central Oregon in the Cascade Range. Needle casts *(Lophodermium uncinatum*, *Phaeocryptopus nudus*, *Virgella robusta)* and rusts *(Uredinopsis* spp.) are common on reproduction in some localities in British Columbia.

Thinning studies on the west coast of Vancouver Island indicated that Pacific silver fir is more susceptible to *Heterobasidion annosum* root and butt rots than are western hemlock, Douglas-fir, or Sitka spruce. Airborne infection of Pacific silver fir stumps was not seasonal as in other species, and infection rates were high throughout the year *(29)*. Pacific silver fir is also one of the Northwest conifers most susceptible to laminated root rot *(Phellinus weiri)* *(27)* and shoestring rot *(Armillaria mellea)*.

Overmature Pacific silver firs are highly prone to heart rot, primarily by the Indian paint fungus *(Echinodontium tinctorium)* and the bleeding conk fungus *(Haematostereum sanguinolentum)*. In British Columbia, Pacific silver firs were free of decay to age 75; then incidence increased with age to 11 percent at 275 years, 40 percent at 375 years, and 100 percent in trees more than 400 years *(6)*. Released advance regeneration scarred by logging is rarely infected by heart rot fungi. In one instance, *E. tinctorium* was nearly absent in young stands 30 years after release, even though adjacent unlogged stands were heavily infected. Lack of suitable branch stubs for entry by fungi and rapid closing of wounds because of accelerated growth are believed to prevent infection *(20)*.

Deterioration is rapid after logging, windthrow, or death caused by insects or diseases. Within 5 years of death, loss in cubic volume can be from 50 to 100 percent. Primary decay fungi on dead wood are *Fomitopsis pinicola*, *Ganoderma applanatum*, *Hirschioporus abietinus*, and *Poria subacida*.

Special Uses

Pacific silver fir is marketed with western hemlock and is typically used for construction framing, subflooring, and sheathing. It is commonly used for construction plywood even though it is not as strong as Douglas-fir. Because of its light color and lack of odor, gum, and resin, Pacific silver fir is well suited for container veneer and plywood. It is occasionally used for interior finish and is suitable for poles. Good yields of strong pulp can be produced by both mechanical and chemical processes. It is a minor Christmas tree species, and its boughs are occasionally used for decorative greenery.

Because Pacific silver fir is common on midslopes of the Cascade Range, it is a large component of many municipal watersheds, wilderness areas, and recreation areas. Its beauty and ability to withstand or respond to human impact make it a suitable species for multiple-use management.

Genetics

Despite its extensive range, Pacific silver fir is not a highly variable species. Cortical oleoresin analyses of sample trees from northern California to the Alaska border revealed no chemical variants, and variation among populations was similiar to that within populations *(51)*. Similar results were obtained from analyses of bark blister and leaf and twig oils.

No artificial hybrids of Pacific silver fir and any other species have been described. It does not hybridize with any of its true fir associates even though pollen shedding and cone receptivity periods may overlap in some localities *(7)*. Some morphological intermediates of Pacific silver fir and subalpine fir have been described, but these proved not to be hybrids *(36)*.

The only known cultivated variety of Pacific silver fir is *Abies amabilis* var. *compacta*, a dwarf form that has current branches 2 to 3 cm (0.8 to 1.2 in) long.

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Abies balsamea (L.) Mill. Balsam Fir

Pinaceae Pine family

Robert M. Frank

Balsam fir *(Abies balsamea)* is one of the more important conifers in the northern United States and in Canada. Within its range it may also be referred to as balsam, Canadian balsam, eastern fir, and bracted balsam fir. It is a small to medium-sized tree used primarily for pulp and light frame construction, and it is one of the most popular Christmas trees. Wildlife rely extensively on this tree for food and shelter.

Habitat

Native Range

In Canada, balsam fir (fig. 1) extends from Newfoundland and Labrador west through the more northerly portions of Quebec and Ontario, in scattered stands through north-central Manitoba and Saskatchewan to the Peace River Valley in northwestern Alberta, then south for approximately 640 km (400 mi) to central Alberta, and east and south to southern Manitoba.

In the United States, the range of balsam fir extends from extreme northern Minnesota west of Lake-of-the-Woods southeast to Iowa; east to central Wisconsin and central Michigan into New York and central Pennsylvania; then northeastward from Connecticut to the other New England States. The species is also present locally in the mountains of Virginia and West Virginia *(23,30)*.

Balsam fir grows from sea level to within 15 to 23 m (50 to 75 ft) below the 1917 m (6,288 ft) summit of Mount Washington in the White Mountains of New Hampshire. At this elevation prostrate balsam fir is found in sheltered areas *(1)*.

Climate

Balsam fir grows best in the eastern part of its range in southeastern Canada and the Northeastern United States. This area is characterized by cool temperatures and abundant moisture. Growth is optimum in areas with a mean temperature of 2° to 4° C (35° to 40° F), a January average ranging from -18° to -12° C (0° to 10° F), a July mean temperature ranging from 16° to 18° C (60° to 65° F), and mean annual precipitation ranging from 760 to 1100 mm (30 to 43 in) *(1)*.

The mean annual temperature within the range of balsam fir varies from -4° to 7° C (25° to 45° F). Mean annual precipitation records show as much as 1400 mm (55 in) to as little as 390 mm (15 in). The amount of growing season precipitation is from 150 to 620 mm (6 to 25 in) *(1)*. There are 80 to 180 frost-free days and about 110 days for optimum growth *(1)*.

Soils and Topography

Balsam fir grows on a wide range of inorganic and organic soils originating from glaciation and generally falling within the acid Spodosol, Inceptisol, and Histosol soil orders. These are characterized by a thick mor humus and a well-defined A_2 horizon, usually gray in appearance because of leaching, and commonly caused by abundant rainfall, cool climate, and coniferous cover. Many of the glacial till soils in New England are shallow and have a compact layer about 46 cm (18 in) below the surface *(11)*.

Soil moisture was the most important predictor of site index in a study in Newfoundland. Soil nutrient status and topography, in that order, were of lesser importance. Glacial tills, often shallow, cover much of the area *(27)*.

Balsam fir has been reported as growing on soils of a wide range of acidity. In the northern Lake States it is most common on cool, wet-mesic sites with pH values between 5.1 to 6.0 *(19)*. Optimum growth occurs on soils where the pH of the upper organic layers is between 6.5 and 7.0 *(1)*. On gravelly sands and in peat swamps, growth is comparatively slow *(41)*.

Associated Forest Cover

Tree species associated with balsam fir in the boreal region of Canada are black spruce *(Picea mariana)*, white spruce *(Picea glauca)*, paper birch *(Betula papyrifera)*, and quaking aspen *(Populus tremuloides)*. In the more southerly northern forest region (fig. 2), additional associates include bigtooth aspen *(Populus grandidentata)*, yellow birch *(Betula alleghaniensis)*, American beech *(Fagus grandifolia)*, red maple *(Acer rubrum)*, sugar maple *(Acer saccharum)*, eastern hemlock *(Tsuga canadensis)*, eastern white pine *(Pinus strobus)*, tamarack *(Larix laricina)*, black ash *(Fraxinus nigra)*, and northern

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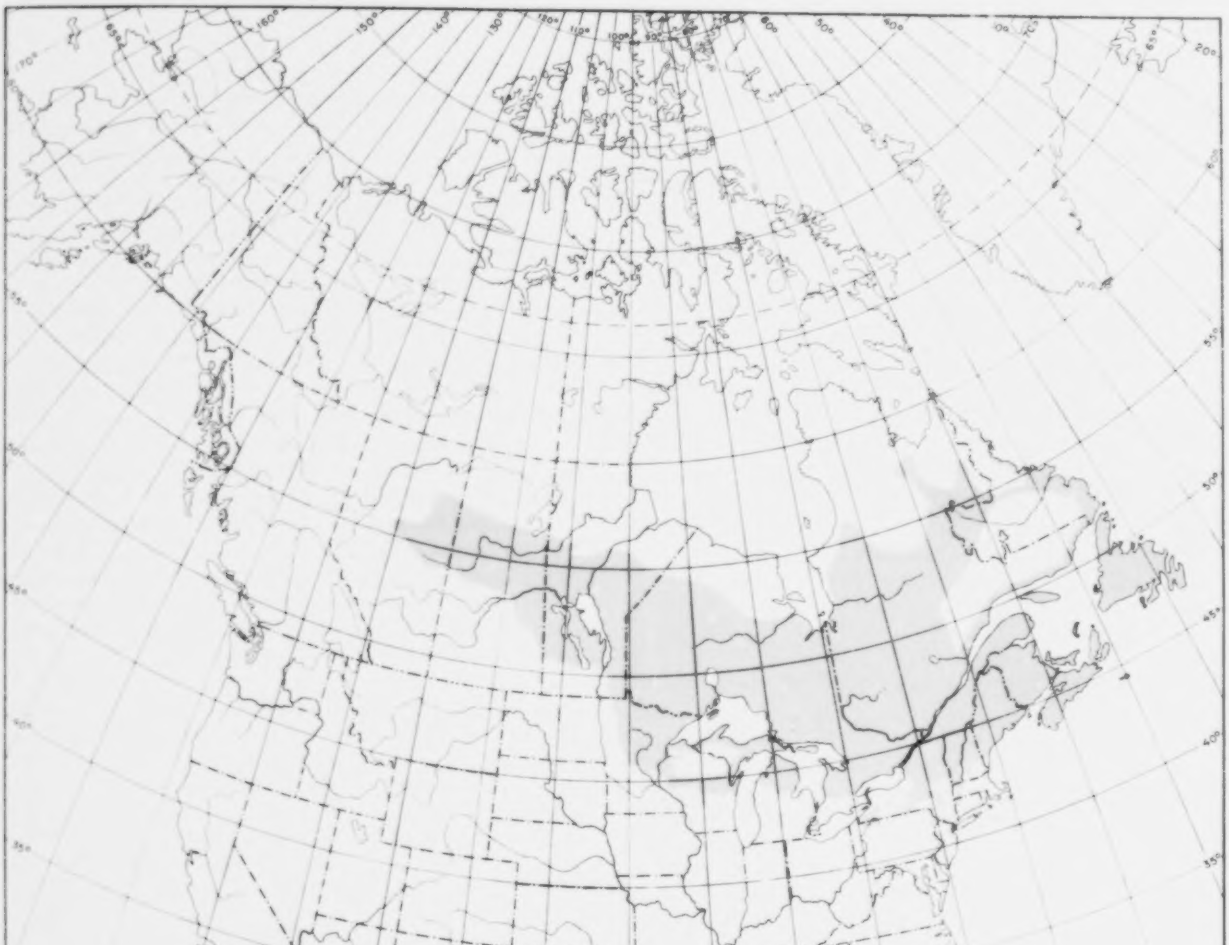

120°
115°
110°
105°
100°
95°
90°
85°
80°
75°
70°
1984

Figure 1—*The native range of balsam fir.*

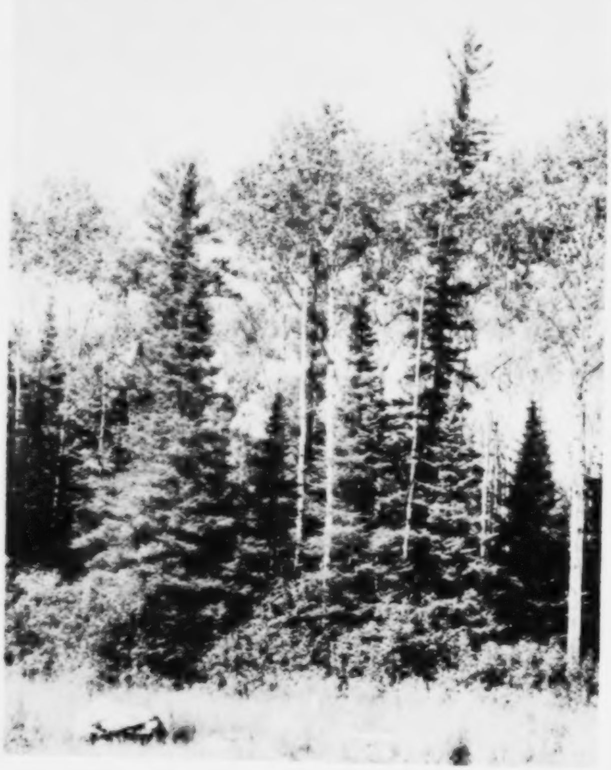

Figure 2—*Balsam fir stand with overstory of aspen. Many acres of this type are found in northern Minnesota.*

white-cedar *(Thuja occidentalis)*. Red spruce *(Picea rubens)* is an important associate in New Brunswick and Maine. Occasional associates are balsam poplar *(Populus balsamifera)*, gray birch *(Betula populifolia)*, red pine *(Pinus resinosa)*, jack pine *(Pinus banksiana)*, and American elm *(Ulmus americana)* *(10)*.

Pure stands of balsam fir or stands in which balsam fir is the major component of growing stock make up the forest cover type Balsam Fir (Society of American Foresters Type 5) *(10)*. Balsam fir is also a major component in two other eastern forest cover types: Red Spruce–Balsam Fir (Type 33) and Paper Birch–Red Spruce–Balsam Fir (Type 35). It is an associated species in 22 eastern forest cover types and in 4 western forest cover types.

Common shrubs associated with balsam fir include beaked hazel *(Corylus cornuta)*, mountain maple *(Acer spicatum)*, Labrador-tea *(Ledum groenlandicum)*, Canada yew *(Taxus canadensis)*, red raspberry *(Rubus idaeus* var. *strigosus)*, sheep-laurel *(Kalmia angustifolia)*, and hobblebush *(Viburnum lantanoides)* *(10,41)*.

Among the herbaceous plants commonly found under balsam fir are twinflower *(Linnaea borealis)*, bunchberry *(Cornus canadensis)*, starflower *(Trientalis borealis)*, creeping snowberry *(Gaultheria hispidula)*, sedges *(Carex* spp.), common woodsorrel *(Oxalis montana)*, bluebead lily or cornlily *(Clintonia borealis)*, painted trillium *(Trillium undulatum)*, cinnamon fern *(Osmunda cinnamomea)*, sweetscented bedstraw *(Galium triflorum)*, Canada mayflower *(Maianthemum canadense)*, and spinulose woodfern *(Dryopteris spinulosa)*.

Certain associations of shrubs, herbs, and mosses indicate forest site quality *(41)*. The four main indicator associations, designated as *Hylocomium/Hypnum*, *Cornus/Maianthemum*, *Oxalis/Cornus*, and *Viburnum/Oxalis* indicate, in the order listed, increasing productivity of site and increasing proportions of shrubs and hardwood trees in natural stands. Only the *Hylocomium/Hypnum* sites are likely to be occupied by pure balsam fir.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Exposure to light influences flowering in balsam fir. In New Brunswick, female strobili were observed on 83 percent of dominant, 59 percent of codominant, and 6 percent of intermediate trees. None were found on suppressed trees *(41)*.

Balsam fir is monoecious. In spring, 1 year before pollination, male (staminate) and female (ovulate or pistillate) strobili differentiate from flower buds. The strobili are microscopically recognizable at this time. Male strobili usually are distinguishable before the female strobili because they initially develop more rapidly. Flower buds usually open in late May or early June before vegetative buds *(41)* but have been reported as flowering as early as late April *(42)*.

Male strobili, yellowish-red and tinged with purple, develop in the axils of leaves along the undersides of the 1-year-old twigs, usually in dense clusters. Their position in the crown is mostly within 5 m (15 ft) of the top and is almost always below the female strobili. Female strobili are purplish and are found singly or in small groups, confined to the top 1.5 m (5 ft) of the crown. They are located on the upper side of the twig and, like the male strobili, develop on the previous year's twig. Flower production is best on the outer end of branches *(41,42)*. At maturity, male flowers are about 3 mm (0.1 in) long; female flowers are about 25 mm (1.0 in) long *(1)*.

Pollen grains are yellow; when developed, their average diameter is 90 μ (0.00354 in). In one series of observations in Ontario, fertilization occurred on June 25 *(1)*. The mature fruit is an erect cone 5 to 10 cm (2 to 4 in) long with short, round, irregularly notched scales and pointed tips. There are thin, closely overlapping fan-shaped scales near the center of the cone. The cone matures and ripens during the first fall in late August and early September. The scales and shorter bracts drop away with the seeds, leaving the central axis, which can persist for many years.

Seed Production and Dissemination—Regular seed production probably begins after 20 to 30 years. Cone development has been reported for trees 15 years of age and younger and only 2 m (6.6 ft) tall. Good seed crops occur at intervals of 2 to 4 years, with some seed production usually occurring during intervening years *(1)*. On the average, 35 L (bushel) containing 1,000 to 2,000 cones weighs approximately 16 kg (35 lb) and yields 1000 to 1200 g (35 to 42 oz) of cleaned seeds. The number of cleaned seeds per kilogram (2.2 lb) ranges from 66,000 to 208,000 and averages 131,000. These are about 134 seeds per cone *(42)*. The seed yield of balsam fir ranged from 5.6 to 20.2 kg/ha (5 to 18 lb/acre) during several good seed years in Ontario *(1)*. Over a 37-year period, annual seed production in this area averaged 1,950 seeds per square meter ($181/\text{ft}^2$) *(15)*.

The period of balsam fir seedfall is long and dissemination distances vary. Seedfall begins late in August, peaks in September and October, and continues into November. Some seeds fall throughout the winter and into early spring. Most of the seeds are spread by wind—some to great distances over frozen snow—and some are spread by rodents. Although seeds may disseminate from 100 m (330 ft) to more than 160 m (525 ft), effective distances are 25 m to 60 m (80 to 200 ft) *(1,11,28)*. Many seeds falling with the cone scales land close to the base of the tree.

Balsam fir seeds have dormant embryos and should be stratified in moist sand at about 5° C (41° F) for at least 30 days before planting. Germination is epigeal *(42)*.

Seedling Development—Within the range of suitable temperatures, moisture is more important than light for germination. In fact, light intensities of only 10 percent of full sunlight result in successful germination *(1)*. The low capacity of planted balsam fir seeds to germinate may be attributed in part to seed injury during the cleaning process. The age of the tree may also contribute to the viability of seeds. A study in Michigan *(41)* showed that germination was highest for a 41-year-old tree (68 percent), varied for trees 30 years old (8 to 57 percent), and was lowest for trees 155 years old (10 percent). Testing of 32 commercial seed lots showed average germination of about 26 percent with a range of 4 to 62 percent *(42)*. Once the seed reaches the ground, its viability diminishes quickly and is gone within 1 year *(13)*. It has been suggested, however, that in cold swamps viability of some seeds is retained for 2 to 3 years *(1)*.

Most germination occurs from late May to early July. Survival the first winter is questionable if germination occurs after mid-July *(1)*. If enough moisture is available, almost any seedbed type is satisfactory, but mineral soil—neither too sandy nor too heavy—with some shade is best. Litter and humus are poor seedbeds, especially if moisture is inadequate or light is excessive. Competition, often severe, makes heavy sod the poorest seedbed *(11)*.

A thick layer of duff exceeding about 8 cm (3 in) is less favorable for balsam fir but even worse for the slower growing associated spruces. Balsam fir seedlings may have a heavy central root, much like a taproot, that extends to the bottom of the humus layer and then splits into several laterals. In general, balsam fir roots grow more rapidly and penetrate deeper than red spruce roots. Where seasonal root elongation of young balsam fir growing in humus averaged 10.6 cm (4.2 in), red spruce was 7.6 cm (3.0 in), and white spruce 9.0 cm (3.5 in), or 39 percent and 18 percent less, respectively *(1)*.

Because the surface of thick duff usually dries out, there may be some delayed germination as late as August. Few seedlings become established, however. The closer seeds lie to mineral soil, the greater the initial establishment of seedlings.

Seedlings starting in the open may sustain heavy mortality when surface temperatures exceed 46° to 54° C (115° to 130° F) or when there is drought or frost heaving. Seedlings may also be smothered or crushed by litter, ice, snow, and hardwood leaves. Losses after the first year usually are minor. As seedlings develop, light at intensities of at least 50 percent of full sunlight are necessary for optimum growth *(11,41)*. Damage caused by late spring frost to new foliage of young seedlings is seldom severe.

Balsam fir seedlings about 15 cm (6 in) tall can be considered to be established *(11)*, especially if secondary branching has occurred. Early growth is then determined largely by the amount and character of dominant competition. Bracken, raspberry, and hardwood sprouts—especially the maples—are the chief competitors on heavily cutover lands in the Northeast. These species may increase dramatically when the original basal area is reduced by 50 percent or more and may dominate the site for 10 to 25 years *(2)*. Unless there has been some soil disturbance, there will be little regeneration of balsam fir and spruce immediately following logging *(45)*. Both balsam fir and the spruces can survive many years of suppression and still respond to release *(11,41)*. The space required for the continual development and establishment of new seedlings probably exceeds that created by the removal of individual trees. To ensure successful regeneration relatively small groups of trees should be removed initially *(12)*.

Vegetative Reproduction—Layering is not an important means of regeneration except for prostrate balsam fir growing in the more northern and mountainous locations such as Isle Royale in Lake Superior, and the White Mountains of New Hampshire. Layering also occurs in open swamps and deep mossy areas and under white pine and jack pine overstories. Trees of any age apparently may layer. Second generations, vegetatively produced, develop when connecting tissues decay and separate *(1)*.

Balsam fir apparently grafts easily *(41)*. In a study in New York, greenhouse grafts were 85 percent successful and field grafts were 80 percent successful. One attempt to air-layer balsam fir was unsuccessful *(1)*. Balsam fir Christmas trees are stump cultured from lateral branches or adventitious shoots.

Sapling and Pole Stages to Maturity

Growth and Yield—Balsam fir at maturity is small to medium size, depending on location and growing conditions. In general, heights range from 12 to 18 m (40 to 60 ft); diameters range from 30 to 46 cm (12 to 18 in) at breast height *(41)*. Where growth is optimum, as in the Green River watershed in New Brunswick, some trees can reach 27 m (90 ft) in height and 75 cm (30 in) in d.b.h. The reported record d.b.h. for balsam fir is 86 cm (34 in). Maximum age is about 200 years *(1)*. How large or how fast balsam fir grows, or how much a stand of balsam fir will yield is related to site factors such as biotic, climatic, and soil conditions, and to age. The condition of the tree or stand and the composition and structure of the stand also influence growth.

Diameter growth was related to vigor and crown length-to-height ratio in a study in Maine. Balsam fir with high vigor and a ratio of at least 0.7—the proportion of live-crown length to total tree height—averaged 6.1 cm (2.4 in) of growth in d.b.h. in 10 years. Less vigorous trees with smaller crown-length ratios ranged downward to an average of 1.0 cm (0.4 in) of growth in 10 years. Vigorous trees with room to grow attain a d.b.h. of at least 25 cm (10 in) in about 50 years *(41)*. In uneven-aged stands of several density classes in Maine, balsam fir grew faster in diameter than spruce and hemlock *(35)*.

Data obtained from stem analysis of balsam fir growing on sites of varying quality in northern Maine has shown height growth curves to be polymorphic (fig. 3). Height growth varies with site quality. From these curves the average site index of a stand can be estimated *(16)*. Monomorphic or harmonized site index curves for balsam fir are also available *(17)*.

Balsam fir is a strong contender for space in stands in which it grows. A 20-year record of stands containing balsam fir in the Penobscot Experimental Forest in Maine showed that the periodic annual volume ingrowth of the species, as a proportion of total volume ingrowth, greatly exceeded its representation in the original stands *(12)*. Because of its many natural enemies, however, volume mortality of balsam fir also greatly exceeds its original representation in these stands.

Balsam fir accounted for 35 percent of the average annual net growth in predominantly softwood stands and 32 percent in mixed stands that were extensively managed. These stands were growing at annual rates of 3.5 m³/ha (49.3 ft³/acre) and 2.9 m³/ha (41.1 ft³/acre), respectively *(31)*.

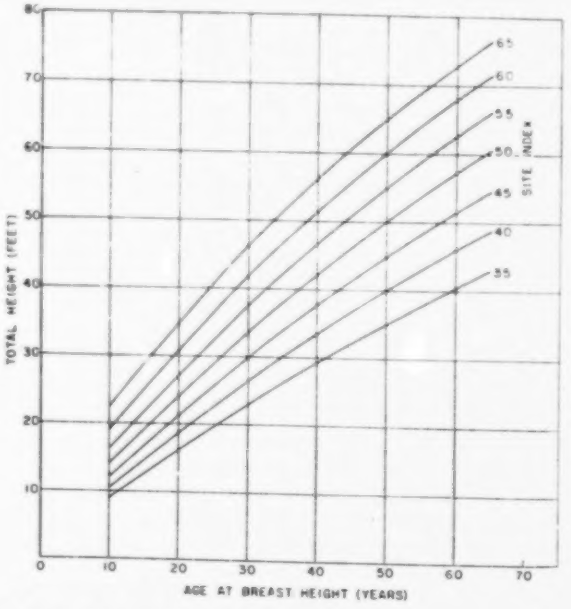

Figure 3—*Polymorphic site index curves (base age 50 years at breast height) for balsam fir in northern Maine, as derived from stem data* (16).

Table 1—Total tree volume (exclusive of roots) of balsam fir greater than 1.5 cm (0.6 in) in d.b.h. by age and site index *(41)*

Age	Site index[1] 12.2 m or 40 ft	15.2 m or 50 ft	18.3 m or 60 ft	21.3 m or 70 ft
yr		*m³/ha*		
20	6	8	9	12
30	50	67	85	102
40	136	182	229	276
50	204	274	344	414
60	245	329	413	497
70	267	360	452	543
80	286	384	481	579
90	300	403	506	609
yr		*ft³/acre*		
20	80	110	135	165
30	720	960	1,210	1,455
40	1,940	2,600	3,270	3,940
50	2,190	3,920	4,920	5,910
60	3,500	4,700	5,900	7,100
70	3,820	5,140	6,450	7,760
80	4,080	5,480	6,870	8,270
90	4,290	5,760	7,230	8,700

[1] Base age 50 years when age is measured at d.b.h.—total tree age is estimated to be 65 years at that time.

Yields in total cubic-foot volume, including stump and top, of all trees larger than 1.5 cm (0.6 in), in d.b.h. are given in table 1. These yields are based on sample plots in even-aged spruce-fir stands, mostly on old fields. They tend to exaggerate the yields that might be expected from the irregular stands that develop after harvesting *(41)*.

Simulating the management and growth of forest stands containing balsam fir is possible because of advances in computer technology. A matrix model, FIBER *(36)*, has been developed for stands in the Northeast. Even-aged and multi-aged stands, containing balsam fir, spruce, northern hardwoods, and other associated species, can be programmed to simulate a range of silvicultural treatments.

In a ranking with both hardwoods and softwoods from around the world, balsam fir is highest with a total aboveground ovendry biomass at age 50 of 184 t/ha (82 tons/acre). Annual increment or annual net primary production averages 10.3 t/ha (4.6 tons/acre) *(20)*. In New Brunswick *(3)*, dry-matter production of balsam fir in pure stands increased dramatically with increases in stand densities of from 1,730 stems per hectare (700/acre) to 12,350/ha (5,000/acre). At an average age from release of 43 years, total aboveground biomass was 96 t/ha (43 tons/acre) for the least dense stand and 143 t/ha (64 tons/acre) for the most dense stand.

Rooting Habit—Balsam fir root systems are mostly confined to the duff layer and to the upper few centimeters of mineral soil *(11)*. Windfall potential is high. Damage from wind is especially likely when the shallow root systems are loosened by heavy rainfall and gusty winds and where timber removals from stands not previously thinned have been poorly conducted. These usually older, dense stands are susceptible probably because root development has been poor.

Root penetration on deep or shallow soils extends to 60 to 75 cm (24 to 30 in) and has been reported to a depth of 137 cm (54 in) in sandy soils in northern Ontario. Lateral roots of balsam fir are usually strongly developed and extend horizontally in all directions to 1.5 m (5 ft) or more *(1)*.

Root breakage and other root damage caused by swaying trees may not be as severe as is commonly thought. Most investigators agree, however, that some root breakage probably occurs because of frost-heaving and swaying. During epidemics of spruce budworm *(Choristoneura fumiferana)*, rootlet mortality can reach 75 percent after 3 consecutive years of defoliation *(1)*.

Balsam fir root grafts are probably common and have been reported frequently. Abrasion of the bark of roots of swaying trees on lowland soils and inter-root compatibility and growth pressure on upland soils apparently account for the majority of root grafts. Infection may spread through grafted roots to damage other balsam fir trees *(1)*.

Reaction to Competition—Balsam fir has a strong ability to become established and grow under the shade of larger trees *(7,11)*. It is classified as very tolerant. Because relative tolerance of species may vary with soil fertility, climate, and age, balsam fir is rated as both more and less shade tolerant than red spruce, and more tolerant than either black or white spruce *(41)*. Intraspecific competition is evident in many sapling and small pole-size stands of pure balsam fir. As these stands mature, dominance usually is expressed. Competition is severe in dense fir thickets, however, and growth rates of individual trees suffer greatly. Other major competition is from the shade-tolerant hardwoods.

In New England, balsam fir is considered a subclimax type, except that it may be a climax species in the zone below timberline. It tends to become climax in Quebec and in the Lake States *(41)*.

Damaging Agents—Many agents act to hinder the growth of balsam fir. Insects and diseases may be devastating. Flammable needles, often close to the ground, shallow root systems, and thin resinous bark make balsam fir susceptible to severe damage and mortality from fire. Susceptibility to wind damage is especially high in old unmanaged stands growing on wet shallow soils. Various species of mice, voles, and birds consume balsam fir seed; birds and squirrels nip buds; and black bears girdle mature trees.

Balsam fir has several insect enemies, the most important by far being the spruce budworm. Despite its name, the spruce budworm prefers fir over spruce; it is most likely to cause heavy damage and mortality in stands that contain mature fir, or that have a dense stocking of fir or a high proportion of fir in relation to other species. Vast budworm outbreaks in eastern North America, perhaps as many as 11 since 1704, have killed tens of millions of cubic meters (hundreds of millions of ft^3) of balsam fir *(6)*. Defoliation causes extensive root mortality. Evidence of budworm attack such as deformation, buried leaders, and decay can be seen 40 or more years later *(1)*. Detailed articles about this important insect pest, with suggestions to alleviate damage, have been written *(7,32)* and a comprehensive bibliography assembled *(25)*.

A classification system for tree vigor and budworm resistance was developed as a guide for selecting spruce and fir trees to remove or retain so as to make spruce-fir stands less vulnerable to spruce budworm attack. Silvicultural techniques designed to increase stand resistance to budworm cannot achieve their aim in the short term; several stand entries over the long term may be required, especially in stands dominated by balsam fir regeneration *(46)*.

The balsam woolly adelgid *(Adelges piceae)*, an introduced insect, is found in Southeastern Canada and in the Northeastern United States. Unless checked by low winter temperatures, populations build up and weaken or kill many trees. Severe stem attack can kill trees within 3 years. The insect also attacks twigs and buds, causing swellings and resulting in loss of new buds, gradual death of twigs and tops, and severe damage to regeneration. An abnormal growth of tracheids caused by insect saliva results in dark, brittle "redwood" *(41)*.

The red heart fungus *(Haematostereum sanguinolentum)*, causes much decay in living balsam fir. It enters almost entirely through injuries to the trunk and living branches *(18)*. Losses from red heart rot are two or three times greater than those caused by butt rots *(11,41)*. Six root and butt rots in balsam fir are economically important. These include the shoestring rot *(Armillaria mellea)*, the two brown cubical rots *(Tyromyces balsameus* and *Coniophora puteana)*, and the three white stringy rots *(Poria subacida, Resinicium bicolor*, and *Scytinostroma galactinium)*. Another root disease of importance is *Serpula himantioides*. *Phaeolus schweinitzii* and *Inonotus tomentosus* also cause a small percentage of the root and butt rot in balsam fir *(18)*. Mechanical or insect-caused wounds to the roots or basal areas of trees provide entrances for these fungi *(41)*. Although the root and butt rots are not responsible for an excessive amount of cull in standing trees, they do weaken trees and make them more susceptible to wind damage, especially if trees are 20 cm (8 in) d.b.h. and larger. The defect caused by these rots is severe enough to be the decisive factor in setting the pathological rotation of fir at about 70 years *(11,18,41)*.

Rot can begin in balsam fir as early as 40 years and increases as the trees get older. More than half generally are infected by the time they are 70 years old. No reliable external indicator of rot is known and even fruiting bodies are rare on living trees. Site seems to have an effect on the incidence and severity of rot; generally, the drier the site, the greater the damage from rot *(41)*.

Specific causes of seedling diseases in nurseries have not been thoroughly reported. The foliage diseases of balsam fir are many but none are economically important to wood production. The same can be said for balsam fir's many stem or canker diseases *(18)*.

The most conspicuous disease of balsam fir is witches' broom, caused by the rust fungus *Melampsorella caryophyllacearum*. Broomed shoots are upright and dwarfed and have yellow needles. Trunk and branch swellings are produced in the shoots *(18)*.

Special Uses

The most important products made from balsam fir wood are pulpwood and lumber *(43)*. The wood of balsam fir, as well as that of other true firs, is creamy white to pale brown. The sapwood has little odor or taste. Wood structure in the true firs is so similar that identification of species is impossible by examining only the wood *(1,43)*.

Balsam fir is pulped by all of the pulping processes. Sulfate and semichemical processes are used most extensively. A fiber length of 3 to 4 mm (0.12 to 0.16 in) is good, as is fiber quality. Because balsam fir is less dense than other major pulpwood species, its yield is lower *(37)*.

The wood of balsam fir is light in weight, relatively soft, low in shock resistance, and has good splitting resistance. Recent testing of several mechanical properties of balsam fir and of red, white, and black spruce indicates strength values for balsam fir generally exceeding those of white spruce. In some tests, strength values were equivalent to or only slightly below the values of red and black spruce *(5,34)*. Nail-holding capacity is low. Balsam fir is very low in resistance to decay *(43)*. The major use of balsam fir lumber is for light-frame construction. Minor uses include paneling, crates, and other products not requiring high structural strength.

Balsam fir provides food or cover for some animals and both food and cover for others. Moose rely on balsam fir in winter when it is a major source of food. The use of balsam fir by deer for cover and shelter is well documented. During severe winter weather, especially in northern areas of the white-tailed deer range, lowland balsam fir stands and spruce-balsam fir swamps are used extensively as winter yarding areas. The fact that these sites usually contain, at best, only small amounts of preferred food suggests their attractiveness as shelter.

Other mammals use balsam fir to varying degrees. The snowshoe hare uses it for cover, and there is some seed and phloem feeding by various species of mice and voles. Red squirrels occasionally feed on balsam fir seed, bark, and wood. They prefer flower buds to vegetative buds. There is some use of wood by beaver for dam building, but little is used as food. Black bear strip bark and lick the exposed surfaces between bark and wood *(1)*.

Balsam fir provides a minor part of the diet for both the spruce grouse and the ruffed grouse. Buds, tips, and needles are consumed, and more feeding occurs in winter than in summer. Thickets of balsam fir provide shelter for both birds *(1)*. The response of bird populations to several forestry practices in stands containing balsam fir has been recorded *(8,40)*. Species composition, the vertical and horizontal structure of the stand, and the extent of spruce budworm infestation influence the composition and density of bird populations.

Balsam fir is not widely planted as an ornamental nor does it offer much potential in areas other than northern New England, Canada, and perhaps the Lake States. Plantings as screens or as windbreaks are successful only when the moisture requirement of the species is met *(1)*. On certain lands and especially on public lands, the unique presence of spruce-fir stands suggests management for esthetic values. In the southern Appalachian mountains, coniferous forests containing balsam fir are managed for watershed protection *(44)*.

Oleoresin, a substance confined to the bark blisters of balsam fir, is used as a medium for mounting microscopic specimens and as a cement for various parts of optical systems. It is also used in the manufacture of medicinal compounds and spirit varnishes *(4)*.

Balsam fir wood is not prized for fuelwood, but industries that use balsam fir for pulp and lumber products are using increasingly larger quantities of wood waste for the production of energy. The heating value of ovendry fir bark is 21 166 600 joules/kg (9,100 Btu/lb) *(26)*.

The fir tree has been a favorite Christmas tree for more than 400 years. It remains among the top three species. In 1980, balsam fir ranked second behind Scotch pine *(Pinus sylvestris)*, commanding 13.9 percent of the market *(38)*. Sheared plantation-grown trees are usually preferred over wildings by retailers and consumers. Wreath-making is another holiday business that rivals that of Christmas tree sales in some areas. Prolonged needle retention after harvest, color, and pleasant fragrance are characteristics of balsam fir that make it attractive for these uses. Fragrance alone accounts for use of the needles as stuffing for souvenir pillows commonly sold in New England gift shops.

Genetics

Population Differences

Variation in balsam fir appears to be clinal and continuous and related to altitudinal gradient and to both east–west and north–south geographic gradients. Variation has been explored in a number of studies.

Balsam fir seedlings grown from seed collected along an elevational gradient in New Hampshire showed a clinal pattern of carbon dioxide uptake with respect to the elevational gradient. This suggests an adaption to temperature through natural selection *(14)*. Another study failed to show that geographical variation in food quality of balsam fir needles is important to the spruce budworm diet but did suggest variation in food quality between locations *(33)*.

In the southern Appalachians the monoterpenes—alpha-pinene and beta-phellandrene—appear to be the best taxonomic characteristics for separating balsam fir from Fraser fir, with alpha-terpene increasing southward and beta-terpene increasing northward. Because no regional variation pattern was evident for wood specific gravity or tracheid length, it has been suggested that only one species of balsam fir with three varieties be recognized in the Eastern United States: *Abies balsamea* var. *bal-*

samea, *Abies balsamea* var. *phanerolepis*, and *Abies balsamea* var. *fraseri (29,39)*.

Balsam fir provenances from eastern portions of the range exhibited more vigor than those from western portions *(24)*. This trait continued through 11 *(22)* and 13 years of total tree age *(9)*. Southern sources tended to flush later, indicating selection for minimizing damage from the balsam gall midge *(Dasineura balsamicola)* and for resistance to late spring frost.

Specific gravity and tracheid length generally vary along an east–west gradient, with eastern sources of lower specific gravity and longer tracheids *(9)*. Generally, trees from slow-growing sources have higher specific gravities and shorter tracheids than trees from fast-growing sources.

Races and Hybrids

No distinct races of balsam fir have been identified. Botanical varieties of balsam fir have been described, *Abies balsamea* var. *phanerolepis* being most important. This variety, the bracted balsam fir, is distinguished by its cone scales, which are shorter than the bracts. The variety *phanerolepis* is found infrequently from Labrador and Newfoundland to Maine and Ontario, and in the high mountains of New Hampshire, Vermont, and New York. It is found locally in northern Virginia and West Virginia *(21,41,42)*, and commonly in several locations in Nova Scotia.

Until the late 1930's, natural or artificial hybrids of balsam fir had not been reported in North America. There were earlier reports, however, of hybrids between balsam fir and Siberian fir *(Abies sibirica)* in Europe *(1)*.

Balsam fir is closely related to Fraser fir *(A. fraseri)*. A taxon of doubtful status, *A. intermedia*, representing a possible cross between the two species, has been reported. This cross has also been reported as *A. balsamea* var. *phanerolepis (1)*. Subalpine fir *(A. lasiocarpa)* also may hybridize with balsam fir where they adjoin in Alberta *(42)*. Workers in Canada apparently have been successful in some instances in hybridizing balsam fir with several species of *Abies*, among them European silver fir *(A. alba)*, alpine fir, and Fraser fir *(1)*. Similar attempts in the United States have been only partially successful.

European horticulturists have propagated many forms of balsam fir for ornamental purposes. Plant form, needle color, and branch length and angle are characteristics usually manipulated. Nineteen such cultivars have been listed *(1)*.

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Abies concolor (Gord. & Glend.) Lindl. ex Hildebr. **White Fir**

Pinaceae **Pine family**

Robert J. Laacke

Long considered undesirable for timber, white fir (*Abies concolor*) is finally being recognized as a highly productive, valuable tree species. White fir reaches its best development and maximum size in the central Sierra Nevada of California, where the record specimen is 58.5 m (192 ft) tall and measures 271 cm (106.6 in) in d.b.h. *(7)*. Large but not exceptional specimens, on good sites, range from 40 to 55 m (131 to 180 ft) tall and from 99 to 165 cm (39 to 65 in) in d.b.h. in California and southwestern Oregon and to 41 m (134 ft) tall and 124 cm (49 in) in d.b.h. in Arizona and New Mexico *(37)*.

Needle form and terpene content vary sufficiently across the wide range of the species to warrant definition of two varieties: the typical var. *concolor*, white fir, often called Rocky Mountain white fir, occupies the eastern and southwestern part of the range; var. *lowiana* (Gord.) Lemm., California white fir, grows in the western range *(31)*. In this paper, "white fir" applies to both varieties.

Habitat

Native Range

The native range of white fir (fig. 1) extends from the mountainous regions of the Pacific coast to central Colorado, and from central Oregon and southeastern Idaho to northern Mexico *(21)*.

Climate

Rocky Mountain white fir grows on high mountains, typically with long winters, moderate to heavy snowpacks, and short growing seasons. Annual precipitation ranges from about 510 mm (20 in) to slightly more than 890 mm (35 in). In the central Rocky Mountains, rainfall is distributed evenly during the summer months. In Arizona and New Mexico, summer tends to be wetter than spring *(37)*.

California white fir grows in cold, high elevations and in warm-to-hot low elevations. Precipitation ranges from 890 mm (35 in) to 1900 mm (75 in) or more per year. California white fir grows best in the southern Cascades and western slopes of the Sierra Nevada, where precipitation is generally between 990 and 1240 mm (39 to 49 in). Locations receiving 1500 mm (59 in) or more are not uncommon, however *(21)*. Essentially, all precipitation occurs during the nongrowing season. Fall and early spring rains are a major portion of the precipitation at lower elevations and winter snowpacks provide more than 80 percent of the moisture at high elevations *(57)*. Occasional summer thundershowers are usually light.

Growth studies on Swain Mountain Experimental Forest, in the southern Cascades of California, indicate that high-elevation stands of California white fir grow best in years with precipitation as low as 38 percent of normal *(45)*. At these elevations low precipitation usually means early snowmelt and a longer growing season *(54)*.

Soils and Topography

Throughout its natural range, white fir grows on a variety of soils developed from almost every kind of parent material. These materials include recent volcanic and igneous rocks of nearly all compositions, large areas of intrusives (mostly granites), and various metamorphics, including serpentine. Sedimentary materials range from limestone, sandstone, and shale to unconsolidated Pleistocene lake deposits *(5,21,22)*. These soils fall into the Inceptisol, Entisol, Alfisol, and Ultisol soil orders. Alfisols are most frequently found at the lower elevations in California where white fir is a component of the Sierra Nevada Mixed Conifer Type.

White fir is generally tolerant of a wide range of soil conditions, nutrient availability, and pH values. It seems to be more dependent on moisture availability and temperature than on soil series. In at least one area of summer-dry Mediterranean climate, productive stands of white fir may utilize water obtained from shattered or otherwise porous bedrock well below the maximum soil depth *(8)*. Growth and development are best on moderately deep and well-drained sandy-loam to clay-loam soils, regardless of parent material. High-elevation fir forests respond strongly to nitrogen fertilizer because low temperatures inhibit decay and natural release of nitrogen from the forest floor *(49)*.

California white fir is moderately sensitive to excess soil moisture and invades high-elevation meadows by growing near older lodgepole pine, taking advantage of relatively dry ground created by the pine roots. A similar pattern of meadow invasion can develop where radiational heat loss on clear, cold

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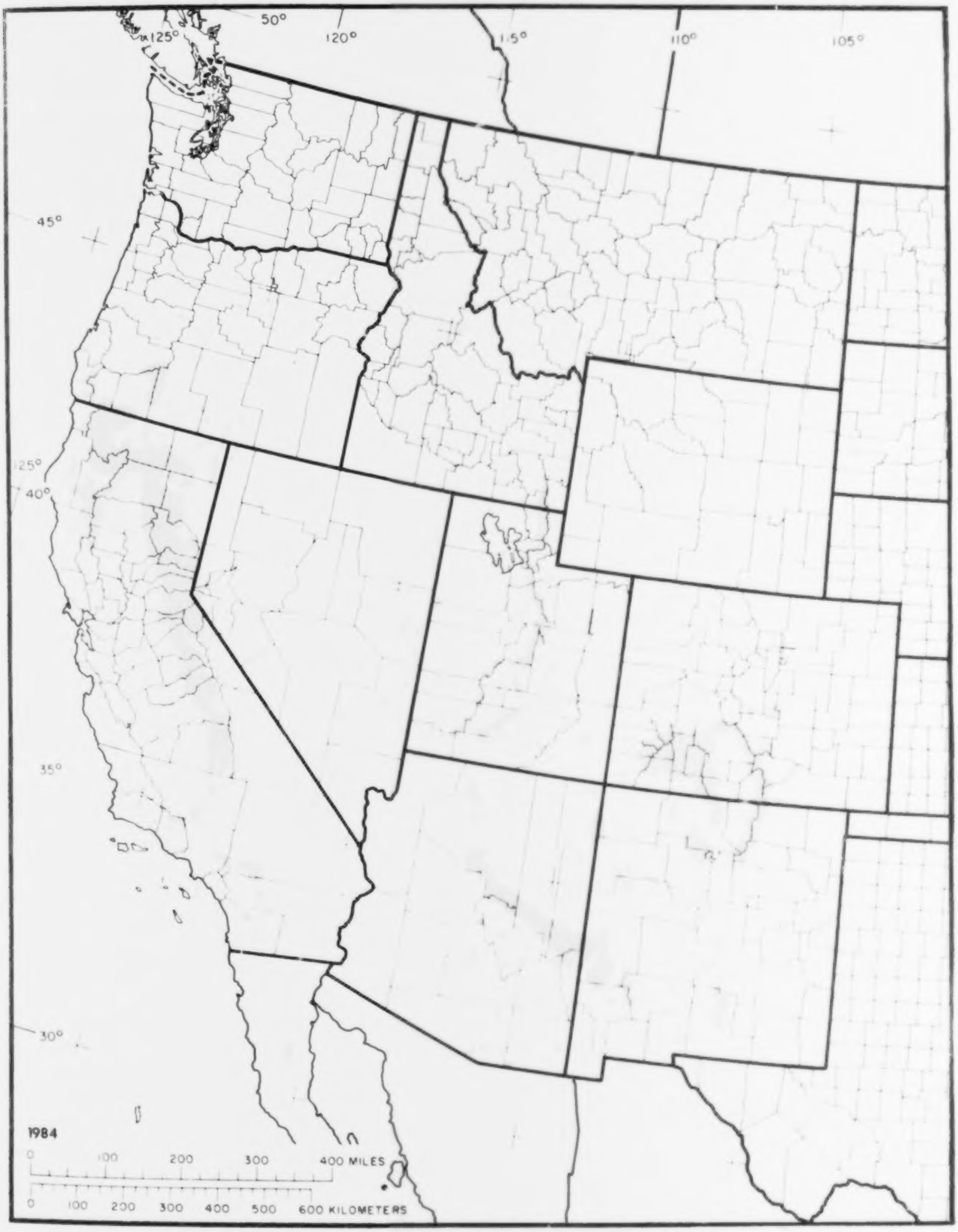
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Figure 1—*The native range of California white fir (left) and Rocky Mountain white fir (right).*

nights is significant. In these situations, the frost-sensitive fir is protected by the pine foliage.

The species grows on various types of terrain, including the extremely steep and unstable slopes of the geologically young Coast Ranges in northwestern California. It develops best on gentle slopes and level ground. Elevations range from a minimum of 600 m (1,970 ft) in the headwaters of the Willamette River of central Oregon to a maximum of almost 3400 m (11,150 ft) east of the continental divide in central Colorado. Lower and upper elevational limits increase from north to south and from west to east as temperatures, distance from the Pacific Ocean, or both increase. Most California white fir in the Sierra Nevada is found at elevations between 1200 and 2100 m (3,900 and 6,900 ft). It grows at elevations of 1500 to 3000 m (4,900 to 9,800 ft) in the San Bernardino Mountains of southern California. Rocky Mountain white fir is found most frequently at elevations between 2100 and 2700 m (6,900 and 8,900 ft) *(21,22,47)*.

Associated Forest Cover

The most common associates of California white fir in the mixed conifer forests of California and Oregon include grand fir *(Abies grandis)*, Pacific madrone *(Arbutus menziesii)*, tanoak *(Lithocarpus densiflorus)*, incense-cedar *(Libocedrus decurrens)*, ponderosa pine *(Pinus ponderosa)*, lodgepole pine *(P. contorta)*, sugar pine *(P. lambertiana)*, Jeffrey pine *(P. jeffreyi)*, Douglas-fir *(Pseudotsuga menziesii)*, and California black oak *(Quercus kelloggii) (21,47)*. In the central Sierra Nevada, white fir is a major associate of the relatively rare giant sequoia *(Sequoiadendron giganteum) (21)*. Species mix varies with elevation, site, and latitude. White fir is more abundant on the cooler, wetter sites.

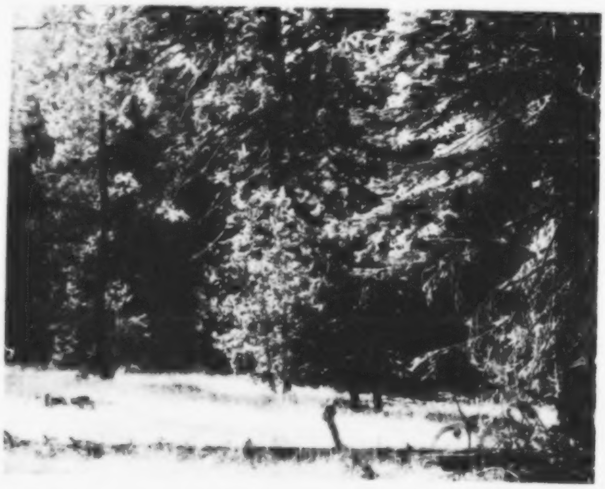

Figure 2—*Small woodland meadow at 1920 m (6,300 ft) in a California white fir—California red fir forest. Downed log in foreground and trees in background are lodgepole pine.*

California white fir is a major climax component throughout the mixed conifer forests within its range. It is displaced successionally only at its northern limits in Oregon, where western hemlock *(Tsuga heterophylla)* and perhaps western redcedar *(Thuja plicata)* replace white fir as a climax species on moister sites *(22)*. At the upper elevational limits of the mixed conifer forest, white fir dominates, occasionally forming pure stands. Still higher, white fir mixes with California red fir *(A. magnifica)* in transition to the red fir type. In the southern Sierra Nevada, white fir in this transition zone generally tolerates canopy closure better and dominates on nutrient-rich sites *(46)*. Lodgepole pine is common in these white fir and mixed fir forests, growing around meadows and along streams (fig. 2). Individuals of Jeffrey pine, western white pine *(P. monticola)*, and sugar pine are scattered through the forest *(47)*. In Oregon, scattered western hemlocks are also found *(22)*.

At low elevations California white fir is an aggressive, tolerant species that appears to have been held in check by frequent natural fires. Extensive fire control efforts, however, have reduced fire frequency. As a result, white fir is becoming a major stand component in California at elevations and on sites where originally it was minor *(48)*. Dense fir regeneration beneath older stands of less tolerant trees is common and threatens a major change in species composition. In many places, especially with giant sequoia, such changes are undesirable, and control measures, including reintroduction of fire, are necessary.

In Arizona and New Mexico, Rocky Mountain white fir (fig. 1) is a major climax component in 11 major habitat types and phases *(42)*. Listed in sequence—from warm and dry low-elevation to cool and moist high-elevation environments—these habitat types include ponderosa pine/Arizona fescue, white fir/Arizona fescue, white fir–Douglas-fir, white fir–Douglas-fir/Gambel oak, white fir–Douglas-fir/Rocky Mountain maple, and blue spruce–Engelmann spruce/forb *(Senecio* spp.). White fir is a minor climax component in the Douglas-fir–southwestern white pine/grass *(Muhlenbergia* spp.), blue spruce–Douglas-fir, and blue spruce/sedge *(Carex* spp.) habitat types. Additional associates are subalpine and corkbark firs. Aspen *(Populus tremuloides)* is a major seral species in many areas.

A variety of woody brush species can assume major importance in much of the white fir range, particularly in mixed conifer zones. Following drastic disturbance, brush can quickly occupy and dominate a site. Common species include mountain whitethorn, deerbrush, and other *Ceanothus* species, manzanita (*Arctostaphylos* spp.), currant and gooseberry (*Ribes* spp.), several chinkapins (*Castanopsis* spp.), and a few oaks (*Quercus* spp.) *(21,22)*. In addition to severely competing for light and moisture *(14)*, at least one *Ceanothus* species contains allelopathic chemicals in its foliage that suppress radicle growth of white fir *(12)*. Mycorrhizal associations are thought to protect white fir roots from allelopathic chemicals produced by bracken fern (*Pteridium aquilinum*) *(1)*. Other species of lesser vegetation that sometimes assumes a significant role includes bearclover (*Chamaebatia foliolosa*) and several grasses. Seeds of some species can lie dormant in the forest floor for as long as 300 years and germinate following removal of forest cover by fire or harvesting. In areas where brush is vigorous, tree seedlings that can survive and grow under brush cover are favored, provided the time between fires is long enough (e.g., 20 years) to allow the fir to establish crown dominance *(13,21,40)*. Pure stands of white fir frequently begin this way.

White fir is represented in at least 14 forest cover types of western North America. Pure stands are White Fir (Society of American Foresters Type 211) *(19)*. It is a major component in Sierra Nevada Mixed Conifer (Type 243) and is also found in the following types:

206	Engelmann Spruce–Subalpine Fir
207	Red Fir
210	Interior Douglas-fir
216	Blue Spruce
217	Aspen
229	Pacific Douglas-fir
231	Port Orford-cedar
237	Interior Ponderosa Pine
244	Pacific Ponderosa Pine–Douglas-fir
245	Pacific Ponderosa Pine
247	Jeffrey Pine
256	California Mixed Subalpine

Life History

Reproduction and Early Growth

Flowering and Fruiting—White fir is monoecious. The reddish male strobili (cones) are generally less than 1.6 cm (0.6 in) long and are densely grouped on the underside of 1-year-old twigs about midcrown. Female cones are borne erect on 1-year-old branches, usually in the uppermost crown although both male and female cones are occasionally found on the same branch. California white fir flowers in May or June and fertilization occurs shortly thereafter. Flowering of Rocky Mountain white fir at the higher elevations may be delayed and extend into July. Female cones reach full size, 7.5 to 13 cm (3 to 5 in) long, in late summer and turn from greenish or purplish to brown when mature *(21,52)*. Cone specific gravity is about 0.85 when mature *(52)*. The seed matures in September, up to 3 weeks before seedfall *(44)*.

Seed Production and Dissemination—Studies of white fir seed and cone production in Oregon, California, and the Rocky Mountains indicate that heavy crops are borne on a 3- to 9-year cycle *(25,29,37)*. Adequate to good crops are produced more often, generally every 2 to 5 years. On extreme sites, cone production patterns may be different.

Seed size varies widely and a kilogram may contain between 18,960 and 39,070 seeds (8,600 to 17,700/lb) *(50)*. Relatively small proportions (20 to 50 percent) of white fir seed are sound, even in good seed years *(21,52)*. Seed numbers, however, can reach 1.5 million/ha (600,000/acre) or more *(24,30)*. Seed production varies with tree age, size, and dominance. The best, most reliable producers are mature, healthy dominants in the 30- to 89-cm (12- to 35-in) d.b.h. range *(29)*. White fir trees can begin bearing cones when only 40 years old and continue beyond 300 years *(45)*. Immature trees can produce heavy seed crops, but their performance is more erratic than that of mature trees *(28)*.

Because cones are borne almost exclusively in the uppermost part of the crown, any top damage caused by insects, diseases, or mechanical agents (for example, wind and snow) directly reduces cone production. Large old trees are prone to such damage. Trees that have lost their tops, however, can frequently develop new terminals and resume cone bearing.

Studies in California indicate that mature dominants along the edge of a clearcutting produce between 1.5 and 6.7 times as many cones as similar trees in adjacent closed stands *(28)*. Regeneration data, also from California, indicate that mature trees left in seed tree or shelterwood cuts increase seed production *(42)*.

Seeds are released as cones disintegrate on the tree. The white fir seed has a relatively short, broad wing for its weight and falls more rapidly than a pine or spruce seed. Because most dissemination is by wind, the distance of seed spread is more limited than that of many associated species. Reliable downwind seed spread into an opening generally is limited to 1.5 to 2 times tree height *(28)*.

Seedling Development—White fir seeds germinate in the spring immediately following snowmelt *(37)* or, where snowpacks are deep, in, on, and under the snow *(23)*. In the Rocky Mountains, white fir germination in spring is in contrast to that of other major species in the mixed conifer type that do not germinate until the summer wet season *(37)*. Seeds that germinate several centimeters above ground in the snowpack rarely survive after snowmelt. Seeds that fall before permanent winter snow cover, therefore, are more likely to produce seedlings. Germination and early growth are best on bare mineral soil. Root systems developed in mineral soil without organic layers are longer, heavier, and have more mycorrhizal root tips than those grown in soil with organic layers *(6)*. White fir seedlings are epigeal.

In general, white fir becomes established best in partial shade, but once established grows best in full sunlight. It is less tolerant of shade than associated true firs (except red fir), is slightly more tolerant than Douglas-fir, and is much more tolerant than pines or oaks *(37,41,56)*. Because white fir can survive and grow beneath heavy brush cover and eventually overtop the brush and dominate the site, many pure stands exist in otherwise mixed conifer areas *(36)*.

Previously it was thought that white fir growth was extremely slow for the first 30 years. It appears now, however, that slow growth beyond 5 years is not inherent and may be caused by environmental conditions, such as prolonged shading and browse or frost damage. White fir is more susceptible to spring frost damage and deer browse than many associated species *(37,41)*.

Radial growth begins before height growth and lasts longer. Height growth begins later in white fir than in associated species at mid-elevations and lasts only about 6 weeks. Occasionally, in California, height growth begins again in late summer. The resulting succulent growth is subject to frost kill. White fir trees from low-elevation seed sources are twice as likely to increase height growth in response to moisture supplied during the summer than are white fir from high elevations or red fir from any elevation *(33)*.

Vegetable Reproduction—White fir shows no tendency to reproduce by sprouting or layering, but cuttings can be rooted with or without hormones. The relative ease with which cuttings from juvenile material can be rooted provides an opportunity to produce genetically selected planting stock at relatively low cost.

Table 1—Volume in white fir stands in California and eastern Oregon and Washington at age 100 *(11,53,59)*

Site index[1] and location	Basal area		Volume	
27.4 m or 90 ft	*m^2/ha*	*ft^2/acre*	*m^3/ha*	*ft^3/acre*
California	108	471	1,372	19,600
Oregon and Washington	80	349	1,066	15,230
18.3 m or 60 ft				
California	91	397	805	11,500
Oregon and Washington	67	291	633	9,039

[1] Average height of dominant trees at base age 50 years

Sapling and Pole Stages to Maturity

Growth and Yield—The capacity of white fir to produce large volumes per unit area was recognized before the species was considered of commercial value. As recently as 1962, white fir was regarded as undesirable in forests managed for timber. The productivity of fully stocked, 100-year-old stands in California *(53,59)* and eastern Washington and Oregon *(11)* on good [Site Index 27 m (90 ft)] and average [Site Index 18 m (60 ft)] sites is evident (table 1). The unusual productivity is possible, at least in part, because this species can grow in stands of high basal area. In mixed-conifer stands, white fir still demonstrates a high level of productivity, although its height growth begins to decrease earlier than that of associated species *(10,17)*.

Rooting Habit—Root systems of mature forest trees, including white fir, have not been the subject of much research. What little is known has been gleaned from observations of windthrown trees. Mature white fir rooting habit appears to be fairly adaptable: deep and intensive where soil conditions permit or shallow and widespread where rocks or seasonal water tables limit effective soil depth. There is no strong tendency to maintain a single deep taproot, although rapid taproot development is critical for survival of new germinants in the dry summer climate.

White fir is susceptible to windthrow following partial cutting, especially when marginal codominant and lower crown classes are left as the residual stand. Root diseases contribute significantly to lack of windfirmness. Root grafting between firs is com-

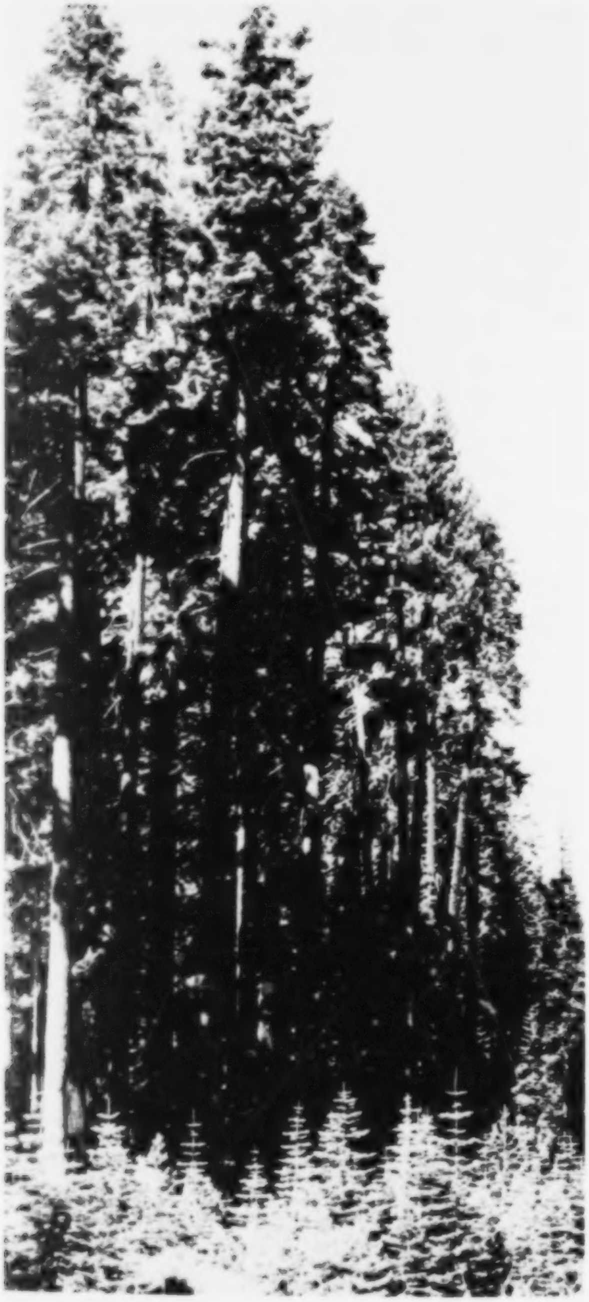

Figure 3—*White fir regeneration in a 20-year-old strip clearcut at 1890 m (6,200 ft) in the southern Cascades.*

mon and is frequently demonstrated by living stumps *(21)*. Root grafting is also a factor in the spread of root rots.

Effects of mycorrhizal associations are beginning to be explored. Early information indicates that these root and fungi relationships are significant, especially in establishment and early growth on poor sites, and that bare mineral soil promotes the association *(6)*.

Reaction to Competition—White fir has several features of major silvicultural significance. The species is classified as shade tolerant, more so than most of its mixed conifer associates *(41)*. Relative shade tolerances of red fir and white fir in the high-elevation transition zone are uncertain. In the northern end of their respective ranges, shade tolerance may be affected by the evident exchange of genetic material with associated species—white fir with grand fir *(A. grandis)* and red fir with noble fir *(A. procera)* *(2)*. White fir is capable of rapid growth to a large size and grows best in full sunlight. It can survive for exceptionally long periods as a suppressed tree and still respond to release by increasing growth dramatically. The time period before growth begins to accelerate varies depending on crown condition at time of release *(36)*. Seed production increases following release even on dominant trees *(38)*.

Because of these features, white fir is a major management consideration in any mixed conifer stand where it is a component. Partial cutting and most shelterwood cuttings favor white fir and increase its importance in the stand. Prescribed burning in areas where white fir is not desired may be the only reasonable way to control its abundance. Underburning in groves of giant sequoia to control young white firs and to create seedbeds for giant sequoia reproduction is a special example.

To manage pure stands of white fir is relatively easy and, with intensive management, young stands can be extremely productive. White fir can be regenerated naturally or artificially. Natural regeneration can be achieved through clearcutting as long as the maximum downwind width of openings does not exceed 1.5 to 2 times the height of trees left as seed sources (fig. 3). Shelterwood cuttings have been successful in establishing natural regeneration *(30)*. On sites where brush competition is a problem, planting under shelterwood has promise. Because of high growth rates in dense, even-aged stands, even-aged management is the likely choice. Uneven-aged management is theoretically possible, however, because of the species' shade tolerance and response to release. The long period of extremely slow growth under shade and the incidence of dwarf mistletoe infestation make uneven-aged management questionable, however.

Damaging Agents—White fir saplings and poles are susceptible to fire damage or kill, but trees become more resistant to both with age and size. White fir is considered more fire resistant than its associated species at high elevations *(37,41)*, but less resistant than its associates at low elevations *(47)*. Fire scars commonly found in old-growth stands, provide an entry court for a variety of disease and decay organisms.

White fir is sensitive to spring and fall frosts. Spring frosts can kill developing buds as well as foliage. Damage to established trees, other than Christmas trees, is not usually significant. On some sites, repeated damage to new fir growth can give a competitive advantage to more resistant species. Cold damage to mature trees takes the form of frost cracks and ring shake. Frost cracks are associated with some rot and decay loss *(9)*.

Sudden rises in temperature during May and early June can cause damage nearly identical to that of spring frosts. Sun-scalding following thinning is rare in mature trees, although young, thin-barked trees are susceptible. When white fir boles are injured, recovery is slow *(9)*.

Compared to its associated species, white fir is moderately susceptible to ozone damage. Although fir grows faster than associated species in southern California, diameter growth is affected by oxidant damage as much as that of Ponderosa pine *(43)*. White fir is more resistant to fluoride damage than Douglas-fir or ponderosa pine *(37)*.

As intensive management of this productive species increases, so will the importance of mechanical injury. Studies in Oregon and California have shown that conventional logging techniques for thinning or partial cutting damaged 22 to 50 percent of the residual stand. Seventy-five percent of these wounds were at ground level, where infection by some decay-causing fungus is almost certain *(3)*. Loss of volume by time of final harvest can be considerable.

Two parasitic plants, white fir mistletoe *(Phoradendron bolleanum* subsp. *pauciflorum)*, a true mistletoe, and white fir dwarf mistletoe *(Arceuthobium abietinum* f. sp. *concoloris)*, cause major damage to white fir *(9)*. In Arizona, Mexico, and the central to southern Sierra Nevada of California, white fir mistletoe is a serious problem on large old trees. Heavy infections cause spike tops, loss of vigor, and increased susceptibility to bark beetle attack. Dwarf mistletoe is a major problem from the southern Sierra Nevada north into Oregon. It is found elsewhere throughout the native range of white fir in coastal and southern California, Nevada, and Arizona *(39,63)*.

One-third of the white fir stands in California are severely infested by dwarf mistletoe and the parasite is present in other forest types that contain white fir. Heavily infected trees suffer significant growth losses and are prone to attack by *Cytospora abietis*, a fungus that kills branches and further reduces growth. Because of reduced vigor, infected trees are more susceptible to bark beetle attack and various diseases *(50,51)*. Heart rots, entering through open mistletoe stem cankers, increase mortality of old-growth trees through stem breakage.

Changes in wood structure in the large stem bulges caused by dwarf mistletoe infections reduce the strength of lumber produced. Current lumber grading practices, however, are not adequate to identify the affected wood *(61)*.

Dwarf mistletoe need not be a problem in young managed stands because three factors make damage subject to silvicultural control. The parasite is host specific: white fir can be infected only by *A. abietinum* f. sp. *concoloris*, which in turn can parasitize only one other fir, grand fir. Small trees (less than 1 m [3.3 ft] tall) are essentially free from infection even in infested stands. Infected young firs free from new overstory infection outgrow the spread of mistletoe if height growth is at least 0.3 m (1 ft) per year *(50)*.

Annosus root rot *(Heterobasidion annosum)* is present in all conifer stands and may become a major disease problem as management of white fir increases. Once established, the disease affects trees within a slowly expanding, circular infection center. Spread from tree to tree is through root contacts. New infection centers begin by aerial spread of spores and infection of basal wounds and freshly cut stumps. In true fir, annosus root rot usually does not kill directly but produces considerable moisture stress and loss of vigor that predispose the tree to attack by bark beetles, notably *Scolytus*. Direct damage resulting from infection is restricted primarily to heart rot of butt and major roots, leading to windthrow and stem breakage *(9)*. Some degree of control is available through silvicultural means and use of borax on freshly cut stumps.

Other rots of major significance include the yellow cap fungus *(Pholiota limonella)*, Indian paint fungus *(Echindontium tinctorium)*, and white pocket rot *(Phellinus pini) (9)*. Yellow cap fungus causes heavy losses from butt rot and enters through fire scars and basal wounds *(9)*. Indian paint fungus is a major heart rot organism. This fungus probably infects fir in the same manner it does western hemlock *(3)*. Entry is through branchlets less than 2 mm (0.08 in) in diameter. The fungus can remain dormant for up to 50 years before being activated by injury to the tree *(18)*. Rot commonly extends 3 m (11 ft) below and 6 m (20 ft) above each characteristic fruiting body *(4)*. No effective control is known although trees less than 40 years old are relatively free of rot because they have so little heartwood. In the white fir–grand fir complex of Idaho, the fungus was found in 97 percent of the trees that had decay. Almost 80 percent of the decay in old-growth grand fir–white fir stands of eastern Oregon and Washington is caused by Indian paint fungus; in California, it is much less common *(9)*.

Insects from seven genera attack white fir cones and seeds. Two cause damage with considerable loss of seed. Seed maggots *(Earomyia* spp.) are the most abundant and damaging. The fir cone looper *(Eupithecia spermaphaga)* covers almost the entire range of white fir and periodically causes considerable local damage *(27)*.

Although many insects feed on white fir foliage, few cause significant damage as defoliators. The most destructive of these is the Douglas-fir tussock moth *(Orgyia pseudotsugata)*. Over most of its range the tussock moth shows equal preference for true fir and Douglas-fir foliage. Epidemic outbreaks, although sporadic, are explosive and damaging. In California, white fir is the preferred host, but outbreaks have not reached the severe levels sustained elsewhere *(27)*. Occasionally, localized outbreaks result in increased stand growth as mortality of subordinate trees "thin" an overdense stand *(59,60)*.

The western spruce budworm *(Choristoneura occidentalis)* is the most destructive defoliator in western North America, causing serious damage in Canada and the Rocky Mountains and Pacific coast regions of the United States. Some outbreaks are short lived, but some continue for 20 years or more. Although initial damage is to new foliage and buds, trees can be completely defoliated in 4 to 5 years. Ultimate damage ranges from minor growth loss to major tree mortality over extensive areas, depending on severity and duration of the outbreak *(27)*.

A similar species, the Modoc budworm *(Choristoneura retiniana* [= *viridis*]), is endemic to the Warner Mountains of northeastern California and southeastern Oregon. Damage to California white fir in the Warner Range has been sporadic and light *(27)*.

The New Mexico fir looper *(Galenara consimilis)* is restricted to New Mexico and can be a serious problem locally on white fir. Weevils of the genus *Agronus* attack foliage of young trees and may cause concern with intensive forest management. Sawflies *(Neodiprion* spp.) are generally not a problem—but are potentially damaging in dense stands of young fir. In California, a species of *Neodiprion* sawfly has reached epidemic levels locally on white fir. White fir needleminer *(Epinotia meritana)* covers the full range of white fir and can cause extensive branch kill predisposing trees to bark beetle *(Scolytus)* attack *(27)*.

Cutworms *(Noctuidae)* can be a problem in nurseries and, more especially, in natural regeneration areas. Cutworms have been responsible for more than 30 percent of the seedling mortality in California *(21,28)*.

The most damaging white fir pest is the fir engraver beetle *(Scolytus ventralis)*. This bark beetle is found over the entire range of white fir and causes serious damage nearly everywhere. Mortality equivalent to an estimated 2.4 million m^3 (430 million fbm) of growing stock is caused each year in California alone. Losses during epidemics are even larger *(27)*. The fir engraver can attack any tree, but those suffering from root rot infections or tussock moth attack are especially vulnerable. In general, anything that reduces tree vigor, such as mistletoes, *Cytospora*, drought, or fire, increases susceptibility to attack *(20)*. Several other bark beetles—including one species of *Pseudohylesinus* and two species of *Scolytus*, the roundheaded borer *(Tetropium abietis)* and the flatheaded fir borer *(Melanophila drummondi)*—frequently join the fir engraver in attacking and killing individual trees. In epidemic conditions, however, mortality is primarily caused by the fir engraver. Maintenance of stand health and vigor is the only known control *(27)*.

Locally, small rodents can cause significant loss of seed and occasionally girdle seedlings. Pocket gophers limit regeneration in many areas, particularly clearcuts, by feeding on fir seedlings during winter and spring. Pocket gophers in combination with meadow voles and heavy brush can prevent conifer establishment for decades *(21,37)*. Pocket gopher damage occurs on trees of all ages and sizes. Feeding on root tissues at the root crown has girdled saplings up to 12.7 cm (5 in) in diameter at breast height (d.b.h.). In at least one place, such feeding has resulted in death of mature trees up to 93.7 cm (36.9 in) d.b.h. *(32)*. Direct control of pocket gopher is difficult and expensive. Indirect control by habitat manipulation offers some possibilities.

Spring browsing of succulent growth by deer and other big game animals can retard height growth for many years. Normally, trees are not killed, and most can grow rapidly once browsing pressure is removed. In managed stands, however, reduced height growth can result in significant economic loss. Damage by big game can be severe in the Southwest. Damage from livestock grazing is limited primarily to trampling and appears to be decreasing as the number of cattle on the open range decreases *(37)*.

Special Uses

White fir is a general, all-purpose, construction-grade wood used extensively for solid construction framing and plywood. A significant portion of the Christmas trees used in California are young white fir. These trees are harvested from natural stands, from regeneration areas where the trees are cultured for as long as 11 years before harvest, and from areas used specifically for Christmas tree production.

Detailed and exact wildlife censuses for large areas do not exist, and any listing of species numbers associated with a major forest type is an approximation. There are, however, about 123 species of birds found in the white fir type of California, 50 of which are associated primarily with mature forests. Perhaps because of the dense nature of most true fir forests in California, there are only 33 species of mammals commonly present and of these only 7 are generally associated with mature forests. Reptiles are represented by 17 species, mostly at lower elevations. Only eight are regularly associated with mature forests *(58)*.

Genetics

White fir is an adaptable and genetically plastic species. Throughout its range, elevational and latitudinal gradients are reflected as changes in stomatal number and arrangement, needle shape, growth rate, phenology, *(34)*, and trachied length *(16)*.

Interspecific crossbreeding is reasonably easy between fir species within the same group (e.g., *A. concolor* and *A. grandis* within Section *Grandes*), but difficult to impossible between sections *(15,35,55)*. In the northern portion of its range, California white fir intergrades and hybridizes freely with grand fir, both being in the Section or group Grandes *(15)*. The species are morphologically, ecologically, and chemically distinct *(20,31)*. They differ in stomatal number and reaction to moisture stress *(63)*. Grand fir grows most abundantly on cool, moist sites and white fir on warmer, drier sites. Grand fir has a higher incidence of heart rot than white fir. Grand fir bark has a red-purple periderm and is high in camphene. White fir bark periderm is yellowish and camphene content is low *(62)*. Hybrid trees are intermediate in all of these characteristics, including incidence of heart rot, which may be more closely related to cool, wet sites than to genetic differences *(26)*.

Over a large area from northwestern California through central Oregon and into central Idaho, identification of the two species is difficult and sometimes impossible. White fir in this region is called "grandicolor."

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Abies fraseri (Pursh) Poir. **Fraser Fir**

Pinaceae **Pine family**

Donald E. Beck

Fraser fir *(Abies fraseri)*, also called southern balsam fir and she-balsam, is a small- to medium-size tree. It is the only fir endemic to the southern Appalachian Mountains. The largest tree on record measures almost 86 cm (34 in) in d.b.h., 26.5 m (87 ft) tall, and has a crown spread of 15.8 m (52 ft). Because of the high elevation at which Fraser fir grows, its primary value is for watershed protection and scenic attraction.

Habitat

Native Range

Fraser fir (fig. 1) has a disjunct distribution, restricted to high elevations in the southern Appalachian Mountains of southwestern Virginia, western North Carolina, and eastern Tennessee.

Climate

Fraser fir grows in a cold, moist climate characterized as a cool-temperate (microthermal) rain forest with a well-distributed mean annual precipitation of 1900 to 2540 mm (75 to 100 in) and average summer temperatures of 16° C (60° F) or less. Average annual temperature varies from 6° C (43° F) at the summit of Mount Mitchell in North Carolina to 9° C (48° F) at the 1524-m (5,000-ft) level in the Great Smoky Mountains National Park. At Mount Mitchell, average January–February temperature varies from –2° C (28° F) to –1° C (30° F), with 147 days below 0° C (32° F). Average July temperature is 15° C (59° F). The frost-free period is 130 to 140 days.

Fog is a very important environmental factor, reducing transpiration and adding measurably to precipitation as fog drip *(21)*. During the growing season, fog may be present on 65 percent or more of the days.

Soils and Topography

There is considerable variation in color, depth, and organic matter content in the soils that support Fraser fir. A typical profile has well-developed organic and A_1 horizons and a B horizon differentiated by color but not by accumulations of clay or iron. Soils are shallow and rocky, with bedrock within 50 to 80 cm (20 to 32 in) of the mineral soils surface *(23)*. The upper 5 to 10 cm (2 to 4 in) of the mineral soil are typically black and greasy, underlaid by a leached gray or yellowish-brown sandy subsoil. Organic surface layers are occasionally thick but usually quite thin, ranging from 2 to 7 cm (0.8 to 2.8 in). The soils are extremely acid; the A horizon pH is about 3.5 and the B horizon pH 3.8 to 4.2. Soil under fir stands above 1920 m (6,300 ft) may be very shallow, with only 15 to 20 cm (6 to 8 in) of a black A horizon lying directly on bedrock *(7)*. Most soils on which Fraser fir grows are Inceptisols.

Fraser fir grows at elevations as low as 1372 m (4,500 ft) on north slopes and protected coves but is found mostly above 1676 m (5,500 ft). It grows at 2037 m (6,684 ft) on top of Mount Mitchell, the highest point in eastern North America.

Associated Forest Cover

Fraser fir is a component of four forest cover types *(10)*: Pin Cherry (Society of American Foresters Type 17), Red Spruce–Yellow Birch (Type 30), Red Spruce (Type 32), and Red Spruce–Fraser Fir (Type 34). It is a minor stand component at the lower elevations, increasing in frequency with altitude to form nearly pure stands at elevations above 1920 m (6,300 ft). At the highest elevation, mountain-ash *(Sorbus americana)* is practically the only canopy associate *(32)*. At middle and lower elevations, red spruce *(Picea rubens)*, yellow birch *(Betula alleghaniensis)*, eastern hemlock *(Tsuga canadensis)*, yellow buckeye *(Aesculus octandra)*, and sugar maple *(Acer saccharum)* are the most common canopy associates *(6,7,8,13,16,32)*. Mountain maple *(Acer spicatum)* and serviceberry *(Amelanchier* spp.) are frequent understory trees.

Shrubs associated with Fraser fir include hobblebush *(Viburnum alnifolium)*, witherod *(V. cassinoides)*, redberry elder *(Sambucus pubens)*, southern mountain cranberry *(Vaccinium erythrocarpum)*, minnie-bush *(Menziesia pilosa)*, southern bush-honeysuckle *(Diervilla sessilifolia)*, catawba (purple) rhododendron *(Rhododendron catawbiense)*, smooth gooseberry *(Ribes rotundifolium)*, and smooth blackberry *(Rubus canadensis)*.

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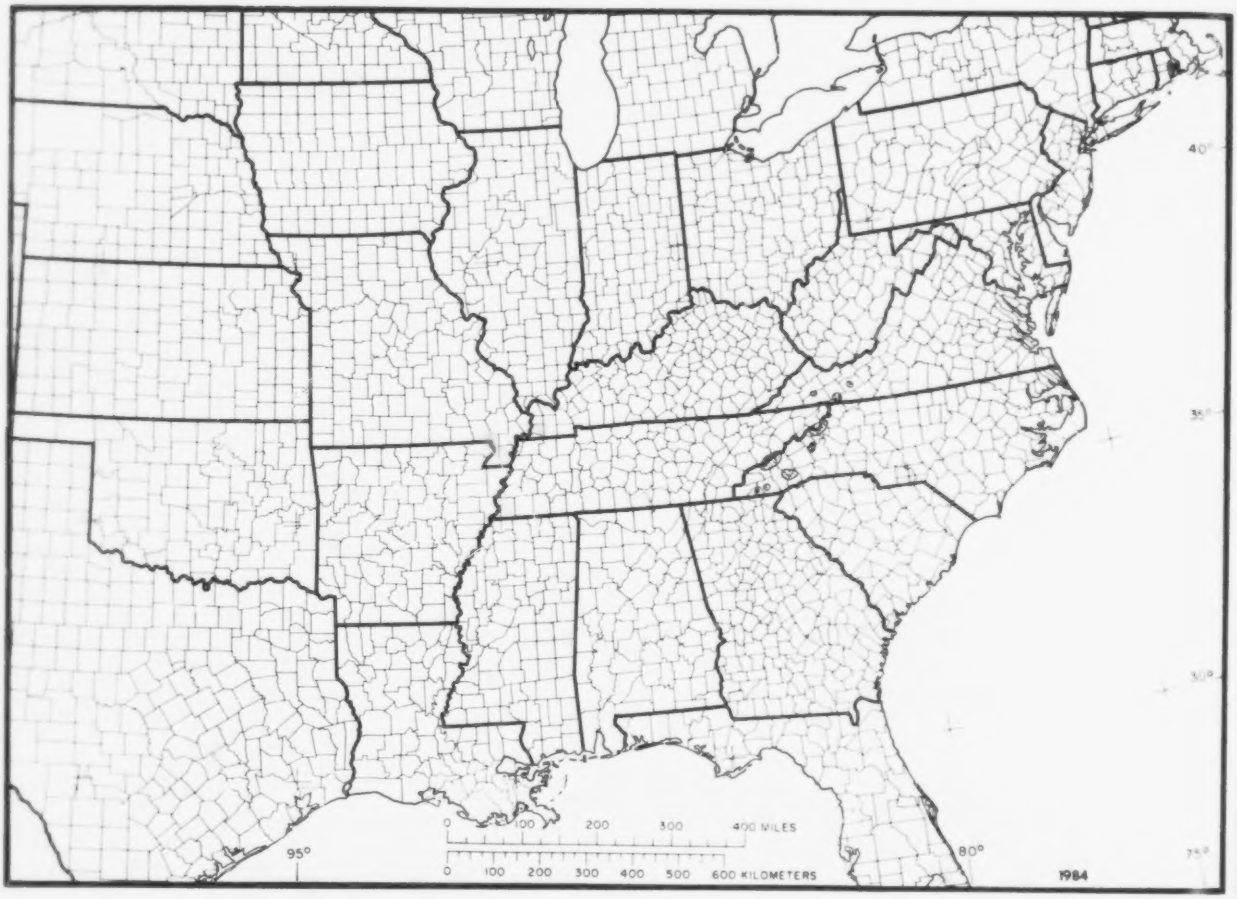

Figure 1—*The native range of Fraser fir.*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Fraser fir is monoecius. Flower buds usually open from mid-May to early June. Female flowers are borne mostly in the top few feet of the crown and on the outer ends of branches. Male flowers are borne below female flowers, but mostly in the top half of the crown. The fruit is an erect cone, 3.5 to 6 cm (1.4 to 2.4 in) long and 2.5 to 4 cm (1.0 to 1.6 in) wide. The strongly reflexed bracts, much longer than the scales, distinguish Fraser fir from balsam fir.

Seed Production and Dissemination—Seed production may begin when trees are 15 years old. Good seed crops occur every other year with light crops in the intervening year. The number of seeds ranges from 119,000 to 174,000/kg (54,000 to 79,000/lb) and averages 134,500 (61,000). The combination of lightweight winged seeds, steep slopes, and high winds makes for good seed dispersal. Seeds may be moved as much as 1.6 km (1 mi), with 50 percent falling over 274 m (900 ft) from their source. Fruit ripens and is dispersed from September through mid-October.

Seedling Development—Germination is epigeal. It approximates 50 percent of sound seeds and appears to be correlated with length of the maturation period. Germination of seeds collected on August 31 was 18 percent but increased to 66 percent for seeds gathered during cone disintegration about September 23 *(26)*. During poor seed years, the yield and quality of seed decrease and insect damage increases *(27,28)*. In a good year, seeds averaged 78 percent filled, with only 3 percent infested by insects. In a poor year, only 36 percent were filled, and 29 percent of that were infested by a seed chalcid, *Megastigmus specularis*.

Fraser fir seeds germinate well on mineral soil, moss, peat, decaying stumps and logs, and even on litter that is sufficiently moist. When seeds germinate on surface litter, the seedlings usually die during dry weather. Moss and peat commonly remain damp, however, and the appearance of moss on the forest floor indicates sufficient moisture to make germination possible with survival throughout the growing season *(19)*.

Stratification of Fraser fir seeds may not be wholly necessary. Stratification for 60 days in peat moss at 3° C (38° F) increased the speed of germination but did not affect the number of seeds germinating. Germination and initial establishment are best under a forest cover. The greatest obstacle to natural reforestation is the desiccation of the moss and peat layer after cutting or fire, followed by surface drying of the mineral soil. Once established, growth is best in full light. Under a dense canopy, Fraser fir may be only 0.6 to 0.9 m (2 to 3 ft) tall in 20 years. In old-growth, all-aged stands, it may take 40 years to attain sapling size. In the absence of shade, it grows much faster. Planted seedlings in cutover forest averaged 2.5 m (8.2 ft) tall in 11 years, with 0.6 m (2 ft) of growth in the 11th year. Under favorable conditions of weed control and fertilization, Christmas tree plantings grow to 1.8 m (6 ft) in 6 to 8 years.

Vegetative Reproduction—Under natural conditions, layering may occur when lower branches come in contact with moist soil, but it is not an important reproductive mechanism. Fraser fir planting stock may be produced by rooting cuttings under controlled temperatures and moisture. A high percentage of stem cuttings from young trees can be induced to root. In one study, rooting was 92 percent in cuttings from 5-year-old trees, compared with 54 percent from 12-year-olds and 29 percent from 22-year-olds. Rooting of cuttings from 32- to 65-year-old trees averaged 4 to 6 percent and varied with crown position *(15)*. It is possible to propagate Fraser fir by stump culture *(32)*. When a Christmas tree is cut, the bottom whorl of limbs is left on the stump. After these turn upward, the most vigorous limb is allowed to develop into another tree.

Sapling and Pole Stages to Maturity

Growth and Yield—Fraser fir is a relatively small tree, rarely more than 24 m (80 ft) tall and 61 cm (24 in) in d.b.h. It is more frequently 15 to 18 m (50 to 60 ft) tall and less than 30 cm (12 in) in d.b.h. Age at natural death is around 150 years *(23)*. Old-growth stands of mixed spruce-fir may carry very high basal areas of 57 to 60 m^2/ha (250 to 260 ft^2/acre) with 1,977 to 2,347 trees/ha (800 to 950/acre) 2.5 cm (1.0 in) in d.b.h. and larger *(7)*. In such stands the fir may average 25 to 28 cm (10 to 11 in) in d.b.h. Yields of mixed spruce-fir over large acreages have been reported to average 210 to 350 m^3/ha (15,000 to 25,000 fbm/acre), some stands yielding 560 to 700 m^3/ha (40,000 to 50,000 fbm/acre) *(24)*. Pulpwood yields averaged 252 to 315 m^3/ha (40 to 50 cords/acre). In such stands, fir constituted one-fourth or less of the total volume.

At the highest elevations where fir forms essentially pure stands, it is most frequently 9 to 12 m (30 to 40 ft) tall, and most canopy stems are 18 to 23 cm (7 to 9 in) in d.b.h. Stems as large as 31 cm (12 in) in d.b.h. are very rare in such stands *(31)*.

Rooting Habit—The root system of Fraser fir is usually shallow because it customarily occupies shallow soils. Root growth is more rapid and rooting depth greater, however, than that of its frequent associate, red spruce *(8)*. Roots are able to penetrate to depths greater than 61 cm (24 in) where soil is available, permitting fir to occupy somewhat drier sites than red spruce *(7)*.

Reaction to Competition—Fraser fir is classified as very tolerant to shade and is considered a climax species. It becomes established and survives for many years under a dense canopy, growing only 2.5 to 5.1 cm (1 to 2 in) per year. When released, it has a marked capacity for recovery. Trees suppressed for 50 years or more have grown rapidly for a time after release *(23)*. Fraser fir tends to form very dense stands which thin slowly and may stagnate in the pole stage *(7)*.

The best means of regenerating fir is probably some method of partial cutting to establish advance reproduction. Harvest methods such as shelterwood or group selection seem ideally suited to accommodate its needs for early shelter but open conditions for later growth. Because of its extreme tolerance, it could probably be handled under a single-tree selection system as well.

Damaging Agents—Because of shallow soils and shallow root systems, Fraser fir is subject to windfall *(7)*. Patches of windthrown trees are a common sight on exposed ridges. Occasional trees on higher ridges are struck by lightning. Heart rots are common in older trees and may increase susceptibility to wind damage. In Christmas tree plantations, twospotted spider mite *(Tetranychus urticae)* can be particularly damaging, causing discoloration and needle loss. On soils with poor internal drainage, root rot caused by the fungus *Phytophthora* spp. becomes a major problem.

All damaging agents are insignificant in comparison to the balsam woolly adelgid *(Adelges piceae)*. It was discovered in North Carolina in 1957 on Mount Mitchell and has since spread to all areas of Fraser fir *(1,2,3,4,9,17,18)*. Mortality progressed rapidly from 11,000 trees in 1958 to about 1.75 million by 1970. Fir mortality has been extensive in all areas except Mount Rogers in Virginia, where infestations dating back to the mid-1960's were first discovered in 1979. Adelgids attack branches, twigs, nodes, and bud bases of fir, but stem attack is the predominant form of infestation. Death usually follows 2 to 5 years after infestation of the bole because of direct translocation impairment.

Further damage by other organisms is associated with attack by the balsam woolly adelgid *(11,12)*. Weakened trees are often attacked by bark beetles, wood wasps, and other wood-boring insects, which also may introduce fungal pathogens *(12)*. Incidence of root rot caused by *Armillaria mellea* was shown to increase with increasing severity of adelgid damage. Damaged and weakened trees are also more susceptible to windthrow and top breakage.

Various chemical insecticides have been found effective against the balsam woolly adelgid, but none has been found technically or economically feasible for use over large forested areas *(14)*. Chemical insecticides are useful, however, for small and accessible stands of high value. Control by a variety of introduced predators has been ineffective.

Openings created by adelgid kill usually contain numerous fir seedlings *(5)*, but the long-term consequences of adelgid attack are unknown. Unless new methods of adelgid control are found, the status of Fraser fir in natural stands is extremely uncertain.

Figure 2—*A pure stand of Fraser fir on Mount Mitchell, NC.*

Special Uses

The remaining stands of Fraser fir have very limited commercial value. However, their location in the cool climate of the loftiest peaks and ridges makes them extremely valuable for watershed protection, as they hold the shallow soil to the steep wet slopes. They are also a unique scenic attraction in a region of growing recreational appeal (fig. 2).

Growing and harvesting this species for Christmas trees and boughs is a multimillion-dollar business in the southern Appalachians. Because of its thick green foliage, beautiful shape, fragrance, and needles that are retained unusually well, Fraser fir is unequaled as a Christmas tree *(29,32)*. It is also used widely as an ornamental yard tree.

Fraser fir seeds and terminal buds are eaten extensively by the red squirrel.

Genetics

Fraser fir was once considered a variety of balsam fir and designated *Abies balsamea* var. *fraseri* Nutt., but the two species are now differentiated on the basis of cone-bract and cone-scale length. *Abies balsamea* has bracts shorter or rarely slightly longer than its scales; *A. fraseri* has strongly reflexed bracts much longer than its scales *(20)*. *Abies balsamea* var. *phanerolepis* in West Virginia and northern Virginia is considered by some to be a natural hybrid of *A. balsamea* and *A. fraseri* because it is intermediate in range and the two have certain common characteristics. Others contend that the disjunct *Abies* subpopulations of the southern Appalachians are relicts of a once-continuous ancestral fir population with clinal variation along a north-south gradient *(22,25,30,33)*.

Artificial crosses of *Abies balsamea* × *A. fraseri* have been made successfully. A cultivar, *A. fraseri* cv. *prostrata*, is a dwarf shrub with horizontally spreading branches used for ornamental purposes *(18)*.

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Abies grandis (Dougl. ex D. Don) Lindl. Grand Fir

Pinaceae Pine family

Marvin W. Foiles, Russel T. Graham, and David F. Olson, Jr.

Grand fir *(Abies grandis)*, also called lowland white fir, balsam fir, or yellow fir, is a rapid-growing tree that reaches its largest size in the rain forest of the Olympic Peninsula of Washington. One tree in that area measures 200 cm (78.9 in) in d.b.h., 70.4 m (231 ft) tall, and has a crown spread of 14 m (46 ft). The species also has historic significance. The famous Barlow Road snub-trees on the south side of Mount Hood in Oregon were grand firs. They were used by early settlers to control the rate of descent of their covered wagons on a particularly steep slope in their trek from east to west. Some of the rope-burned trees are still standing after 150 years.

Habitat

Native Range

Grand fir (fig. 1) grows in the stream bottoms, valleys, and mountain slopes of northwestern United States and southern British Columbia. Its wide geographical distribution is from latitude 51° to 39° N. and from longitude 125° to 114° W. In the Pacific coast region it grows in southern British Columbia mainly on the lee side of Vancouver Island and the adjacent mainland, in the interior valleys and lowlands of western Washington and Oregon, and in northwestern California as far south as Sonoma County. The range in the continental interior extends from the Okanogan and Kootenay Lakes in southern British Columbia south through eastern Washington, northern Idaho, western Montana west of the Continental Divide, and northeastern Oregon. The best commercial stands of grand fir are in the Nez Perce and Clearwater regions of northern Idaho *(9)*.

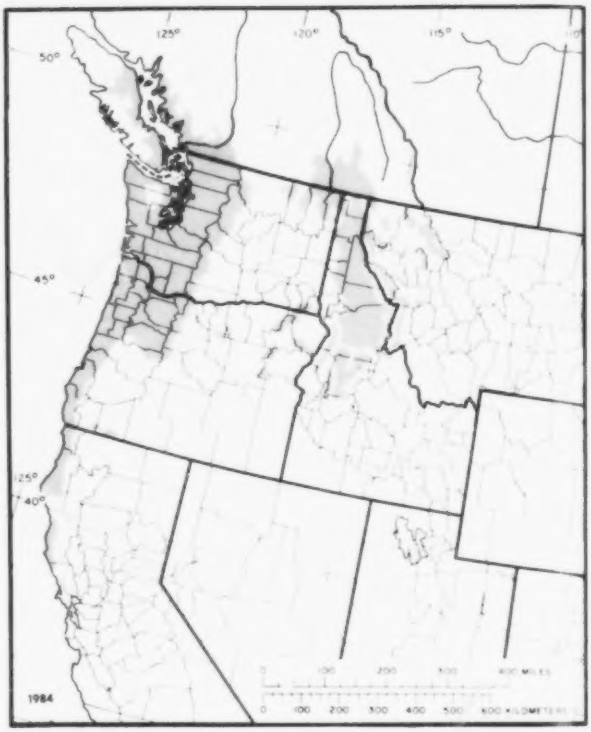

Figure 1—*The native range of grand fir.*

Climate

Grand fir is found on a wide variety of sites. Average annual precipitation in its territory ranges from 510 to more than 2540 mm (20 to 100 in) in western Washington and on Vancouver Island. Annual precipitation in the Blue Mountains of eastern Oregon averages 360 to 990 mm (14 to 39 in). In northern Idaho, average annual precipitation is 510 to 1270 mm (20 to 50 in). Most of this precipitation occurs during winter. Generally 15 to 25 percent of the annual precipitation occurs during the growing season, May through August. On Vancouver Island, where average annual precipitation ranges from 680 to 2820 mm (27 to 111 in), only 50 to 130 mm (2 to 5 in) of rain falls during June, July, and August. Average annual snowfall ranges from a few centimeters on some coastal sites to more than 1270 cm (500 in) in the mountains of the interior *(9)*.

Average annual temperatures range from 6° to 10° C (43° to 50° F); the average growing season temperature is 14° to 19° C (57° to 66° F). The frost-free season varies, ranging from about 60 to more than 250 days, and is very irregular from year to year. Frosts may occur in any month in the interior. The average growing season ranges from only 100 to 140 days in northern Idaho, 185 days on the Olympic Peninsula in western Washington, and 250 or more days in northern California *(9)*.

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Soils and Topography

Grand fir seems to grow equally well on soils derived from a variety of parent materials, including sandstone, weathered lava (rock), or granite and gneiss. In the Pacific coast region and in the Willamette Valley of Oregon it grows most abundantly on deep, rich alluvial soils along streams and valley bottoms and on moist soils provided with seepage. In the inland regions it grows best on rich mineral soils of the valley bottoms, but it also grows well on shallow, exposed soils of mountain ridges and pure pumice soils in central and eastern Oregon, provided moisture is adequate *(9)*. Most of the soils that support grand fir have been classified as Spodosols.

Grand fir grows on Vancouver Island and the adjacent mainland of British Columbia at elevations between sea level and 305 m (1,000 ft). In the southern interior of British Columbia it grows only in the moist valleys of such rivers as the Kootenay, Columbia, and Okanogan and their tributaries. Grand fir is predominantly a lowland species in western Washington, Oregon, and British Columbia. In western Washington it grows in valleys and stream bottoms having high ground-water levels. Elevations of these sites are usually between 180 and 305 m (590 and 1,000 ft). At elevations above 460 m (1,510 ft), grand fir is replaced by Pacific silver fir (*Abies amabilis*). Grand fir is found in western Oregon and in the lowlands of all the river regions, and in the lower west Cascades to an elevation of 915 m (3,000 ft). In northern California it grows from near sea level to about 1525 m (5,000 ft) *(9)*.

In the eastern Cascades of Washington, 915 to 1220 m (3,000 to 4,000 ft) is the upper altitude limit for grand fir, while in the eastern Cascades of Oregon it grows at 1525 m (5,000 ft). In the Inland Empire, including the Blue Mountains of Oregon, it is found as high as 1830 m (6,000 ft) and as low as 460 m (1,500 ft), but usually between 610 and 1525 m (2,000 and 5,000 ft). In the Nez Perce region of central Idaho, it grows well at altitudes of 1220 to 1675 m (4,000 to 5,500 ft) *(9)*.

Associated Forest Cover

Grand fir (fig. 2) is either a seral or climax species in different forest types within its range. On moist sites it grows rapidly enough to compete with other seral species in the dominant overstory. On dry sites it becomes a shade-tolerant understory and eventually assumes dominance as climax conditions are approached.

Grand fir is represented in 17 forest cover types of western North America: it is the predominant species in only one, Grand Fir (Society of American Foresters Type 213) *(26)*. It is a major component of six other cover types: Western Larch (Type 212), Western White Pine (Type 215), Interior Douglas-Fir (Type 210), Western Hemlock (Type 224), Western Redcedar (Type 228), and Western Redcedar–Western Hemlock (Type 227). Grand fir appears sporadically in 10 other cover types.

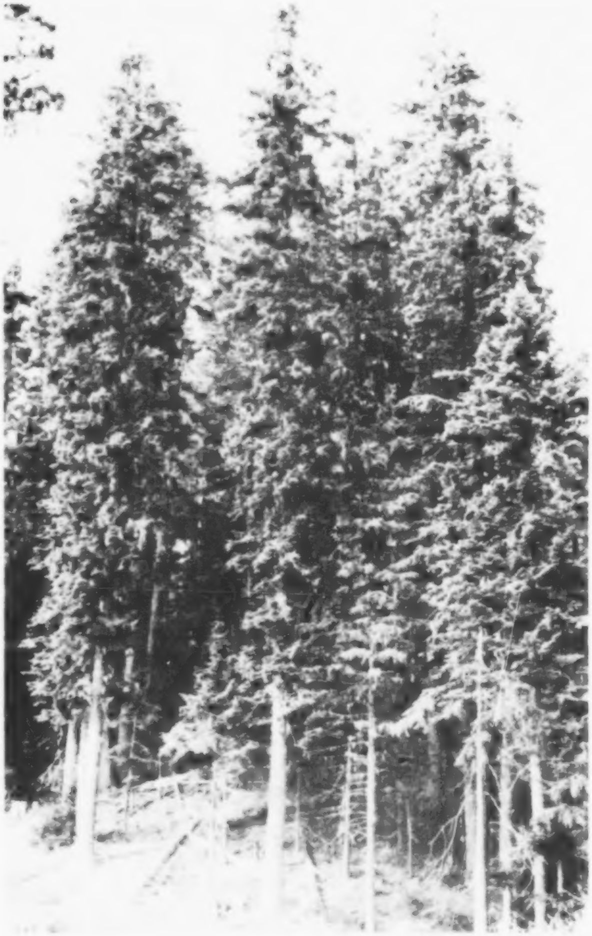

Figure 2—*Mature grand fir trees in the Coeur d'Alene National Forest, ID.*

In northern Idaho, grand fir is the major climax tree species in seven habitat types and is an important seral tree in the *Thuja plicata*, *Tsuga heterophylla*, and *Abies lasciocarpa* series of habitat types *(5)*. The Montana forest ecological classification recognizes an *Abies grandis* series of three habitat types in which grand fir is the major climax tree *(23)*. It is also a minor climax or seral tree in four other types in Montana. In central Idaho, Steele and others

(28) described an *Abies grandis* series that includes nine habitat types and five phases in which grand fir is the climax tree.

The *Abies grandis* zone is the most extensive midslope forest zone in the Cascade Range of Oregon and southern Washington and the Blue Mountains of eastern Oregon. Grand fir is the climax tree species in 12 plant associations *(15,18)*. It is also an important component of the mixed conifer communities in the Willamette Valley and Siskiyou Mountains of Oregon *(16)*. In addition, grand fir grows sporadically in the *Tsuga heterophylla, Picea sitchensis*, and *Abies amabilis* zones in the coastal forests of Washington and Oregon *(11)*.

Grand fir sometimes grows in pure stands but is much more common in mixed coniferous and hardwood forests. In forests east of the Cascade crest, it is associated with western white pine *(Pinus monticola)*, western larch *(Larix occidentalis)*, Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, western redcedar *(Thuja plicata)*, lodgepole pine *(Pinus contorta)*, ponderosa pine *(Pinus ponderosa)*, and in certain areas, Engelmann spruce *(Picea engelmannii)*, subalpine fir *(Abies lasiocarpa)*, black cottonwood *(Populus trichocarpa)*, Pacific yew *(Taxus brevifolia)*, white fir *(Abies concolor)*, incense-cedar *(Libocedrus decurrens)*, sugar pine *(Pinus lambertiana)*, Shasta red fir *(Abies magnifica* var. *shastensis)*, and Oregon white oak *(Quercus garryana)*.

Associates of grand fir in northwestern Oregon, western Washington, and southwestern British Columbia include Sitka spruce *(Picea sitchensis)*, Pacific silver fir *(Abies amabilis)*, and Port-Orford-cedar *(Chamaecyparis lawsoniana)*, in addition to western redcedar, western hemlock, western larch, and Douglas-fir. It also is associated with these coast hardwoods: bigleaf maple *(Acer macrophyllum)*, Oregon ash *(Fraxinus latifolia)*, red alder *(Alnus rubra)*, black cottonwood, and Oregon white oak.

In southwestern Oregon and northwestern California, at the southern limits of the range, grand fir is found with redwood *(Sequoia sempervirens)*, and at higher elevations with Shasta red fir, white fir, noble fir *(Abies procera)*, subalpine fir, and western white pine.

Shrubs commonly associated with grand fir include pachistima *(Pachistima myrsinites)*, bristly black currant *(Ribes lacustre)*, Saskatoon serviceberry *(Amelanchier alnifolia)*, Rocky Mountain maple *(Acer glabrum)*, twinflower *(Linnaea borealis)*, birchleaf spirea *(Spiraea betulifolia)*, huckleberry *(Vaccinium* spp.), Utah honeysuckle *(Lonicera utahensis)*, mallow ninebark *(Physocarpus malvaceus)*, common snowberry *(Symphoricarpos albus)*, baldhip rose *(Rosa gymnocarpa)*, princes-pine *(Chimaphila* spp.), Spalding rose *(Rosa nutkana* var. *hispida)*, oceanspray *(Holodiscus discolor)*, creeping hollygrape *(Berberis repens)*, willow *(Salix* spp.), thimbleberry *(Rubus parviflorus)*, rustyleaf menziesia *(Menziesia ferruginea)*, and pyrola *(Pyrola* spp.).

Herbaceous species commonly found in various associations with grand fir include queenscup *(Clintonia uniflora)*, false solomons-seal *(Smilacina stellata)*, goldthread *(Coptis occidentalis)*, Pacific trillium *(Trillium ovatum)*, sweetscented bedstraw *(Galium triflorum)*, pathfinder (trailplant) *(Adenocaulon bicolor)*, wildginger *(Asarum caudatum)*, Piper anemone *(Anemone piperi)*, violet *(Viola* spp.), sandwort *(Arenaria macrophylla)*, heartleaf arnica *(Arnica cordifolia)*, strawberry *(Fragaria* spp.), rattlesnake plantain *(Goodyera oblongifolia)*, western meadowrue *(Thalictrum occidentale)*, coolwort *(Tiarella* spp.), fairybells *(Disporum oreganum)*, white hawkweed *(Hieracium albiflorum)*, and sweetroot *(Osmorhiza* spp.). Graminoids frequently associated with grand fir are Columbia brome *(Bromus vulgaris)*, pinegrass *(Calamagrostis rubescens)*, western fescue *(Festuca occidentalis)*, and sedge *(Carex* spp.). Additional species are associated with grand fir in the coastal region, where it grows with western hemlock, coastal Douglas-fir, Sitka spruce, and redwood.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Grand fir trees are monoecious; male and female flowers are borne in clusters on branchlets of the previous season's growth in different parts of the same tree. Female flowers, producing cones and seeds, are short, spherical to cylindrical, and stand singly and erect on the uppermost part of the crown. Male flowers, pollen-bearing only, are ovoid or cylindrical and hang singly from the lower side of branches below the female flowers. This arrangement favors cross-fertilization. The cones mature in one season. Time of flowering may vary over several months, depending on temperatures during the weeks preceding flowering. Flowering occurs from late March to mid-May at lower elevations of most coastal locations, and in June at the higher elevations of the inland locations. The cones, mostly yellowish-green and occasionally greenish-purple, ripen from August to September of the same year, and seeds are dispersed approximately 1 month later *(32)*.

Extreme frosts may occasionally inhibit normal cone and seed development. Several species of insects feed on the buds, conelets, and seeds of grand fir, sometimes destroying 10 to 25 percent of the year's seed crop *(9)*.

Seed Production and Dissemination—Seed production begins at about 20 years of age and increases with age, diameter, and vigor of the tree. Eight-year observations of permanent sample plots in Idaho show that grand fir produced the fewest seeds of the species associated with western white pine. Grand fir produced no good crops and only two fair crops, while western white pine produced two good crops and three fair crops. During the same 8-year period, western hemlock produced five good crops and two fair crops *(9)*. In the coastal forests of Washington, grand fir ranked higher than western white pine and intermediate among upper slope species in number of seeds produced per tree *(22)*. Other sources place the interval between good seed crops at 2 to 3 years *(10,32)*.

In the Inland Empire, a good cone crop for grand fir is considered to be more than 40 cones per tree. A fair crop is 21 to 40 cones per tree. Grand fir seeds caught annually in seed traps on two sample plots averaged 42,000/ha (17,000 acre) on the Kaniksu National Forest and 58,100/ha (23,500 acre) on the Coeur d'Alene National Forest. Eight-year observations of seed traps under a 300-year-old stand on the Priest River Experimental Forest yielded 31,600 grand fir seeds per hectare (12,800 acre) annually *(9)*. The yield of cleaned seeds ranges from 26,200 to 63,100/kg (11,900 to 28,700/lb) and averages 40,500/kg (18,400/lb) *(32)*.

When the cones are ripe, the scales fall away and release the large-winged seeds, leaving only the central spike. Seeds are dispersed by the wind and rodents. Most of the seeds are disseminated in the early fall, about 5 percent falling before September 1 and 80 percent falling before the end of October. Seeds sufficient to produce adequate reproduction may be distributed up to 120 m (400 ft) from the parent tree, but the average distance is about 45 to 60 m (150 to 200 ft). Seeds in the duff remain viable through only one overwinter period *(9)*.

Seedling Development—Grand fir seeds germinate in the spring following one overwinter period on the ground. In natural stands, germination is quite variable but is seldom greater than 50 percent because of embryo dormancy, insect infestation, and the perishable nature of the seeds. Seeds are often so heavily infested with insects that an entire crop may be classed as a failure *(9)*.

Stratification under cool, moist conditions speeds germination. Grand fir seeds are typically stratified at 1° to 5° C (34° to 41° F) for 14 to 42 days before nursery sowing in the spring. Results of greenhouse germination tests of grand fir seeds are highly variable. In three sandflat germination tests in the northern Rockies, grand fir had the lowest germination percentage among major associates of the western white pine type *(9)*. Average percentages were grand fir, 12; western larch, 30; Douglas-fir, 41; western white pine, 44; western hemlock, 65; and western redcedar, 73. As with other true firs, germination is epigeal.

In reported tests, germinative capacity ranged from 0 to 93 percent and averaged 50 percent *(32)*. The variability and average grand fir germination are about average for the true firs.

Grand fir seed germination begins in late April or early May on exposed sites and a month later on protected sites where snow lingers late. It is practically completed by July 1 on exposed sites and by August 15 on protected sites. Germination is best on mineral soil, but on seed-tree cuttings, grand fir germinates nearly as well on duff as on any other surface *(9)*.

Studies of seedling survival indicate that more than 30 percent of grand fir seedlings die in the first season, and an additional 10 percent die in the second season. Losses drop off rapidly after the first 2 years, and seedlings 3 years old are fairly well established *(9,24)*. Studies of mortality during the critical first year indicate that early season losses are due principally to biotic agents, especially damping-off fungi. Fungi-caused mortality is very irregular, however. Later in the season as the soil begins to dry and temperatures rise, mortality is due principally to heat from insolation and drought. Surface-soil temperatures are less important under shade or on sheltered sites, and under dense shade or on north slopes high temperatures do not cause death. Grand fir is relatively resistant to heat injury; it is equal to western white pine and Douglas-fir and more resistant than western larch, western hemlock, and western redcedar. Grand fir seedlings are relatively resistant to drought on areas exposed to full sun because deep initial root penetration protects them from drying of the surface soil. On heavily shaded, cool areas, drought is the most important physical cause of seedling mortality because initial root penetration is slow; even shallow drying of the surface soil may cause drought mortality despite ample soil moisture at deeper levels *(9)*.

Initial survival and growth of grand fir are favored by a moderate overwood shade. Under full sun it is largely subordinate to faster growing, shade-intolerant species. Under partial overwood shade, grand fir is aggressive enough to form a dominant part of the reproduction. After 20 to 30 years, it makes most rapid growth in the open *(9)*.

Vegetative Reproduction—No information is currently available.

Sapling and Pole Stages to Maturity

Growth and Yield—Longevity of grand fir is intermediate among true firs; trees 250 years old are common and occasional trees may be more than 300 years old. On optimum sites in the coastal lowlands of Washington, mature grand firs reach heights of 43 to 61 m (140 to 200 ft) at 51 to 102 cm (20 to 40 in) d.b.h.; occasionally they reach 76 m (250 ft) in height and 152 cm (60 in) in d.b.h. *(11)*. Grand fir in the redwood forests of California reaches d.b.h. and heights as great as those attained in the coast Douglas-fir region. In northern Idaho grand fir normally grows to 35 to 46 m (115 to 151 ft) in height at 64 to 102 cm (25 to 40 in) in d.b.h. On the pumice soils of eastern Oregon it attains height of 30 to 40 m (98 to 131 ft) with d.b.h. of 51 to 91 cm (20 to 36 in). On exposed ridges of the Inland Empire, heights of 15 to 21 m (49 to 69 ft) and d.b.h. of 30 to 36 cm (12 to 14 in) are common *(9)*.

The rapid early height growth nearly equals that of Douglas-fir on the Pacific coast and western white pine in Idaho. On Vancouver Island and western Washington sites, growth of 79 to 89 cm (31 to 35 in) per year was reported. Trees 43 m (141 ft) tall at 50 years of age have been measured. In Idaho early height growth of 15 to 20 cm (6 to 8 in) on average sites and 30 to 36 cm (12 to 14 in) on optimum sites has been reported. In the dry pumice soils of eastern Oregon, average juvenile height growth up to 13 cm (5 in) per year has been reported. On these dry sites good height growth is delayed until the taproots reach ground water. At some time in the third decade, height growth receives considerable impetus and annual height growths of 51 to 89 cm (20 to 35 in) or more are common *(9)*.

Among pole-size trees, growth is nearly equal to the more shade-intolerant western white pine and Douglas-fir with which it is commonly associated. Grand fir commonly outgrows the more tolerant western hemlock and western redcedar.

Grand fir has been planted successfully in many European countries, where it is considered one of the most potentially productive species *(2)*. In England, growth of grand fir plantations was compared with that of neighboring plantations of other commonly planted species, and the rate of growth of grand fir at 40 years of age frequently equaled or exceeded that of other species such as Sitka spruce, Norway spruce (*Picea abies*), and Douglas-fir *(2)*.

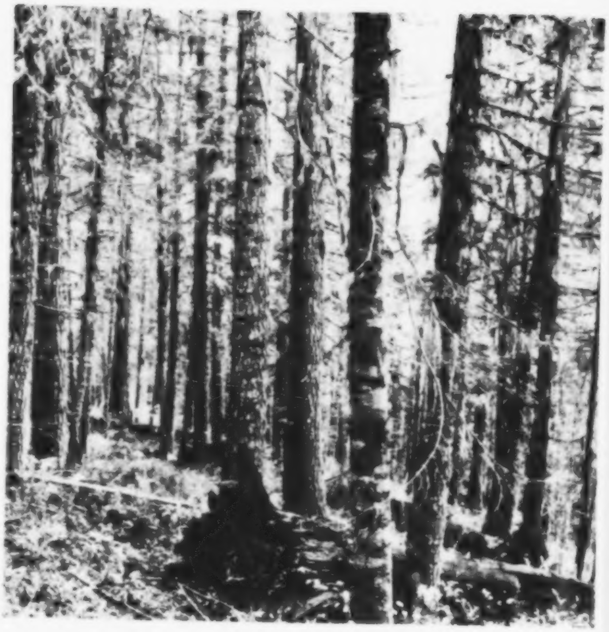

Figure 3—*A 90-year-old grand fir stand, Coeur d'Alene National Forest, ID.*

Grand fir seldom grows in pure stands except in areas of the Clearwater River drainage of north-central Idaho (fig. 3). Therefore, estimates of yields have value mainly in relation to mixed stands. Grand fir ranks among the most productive species in all the associations in which it grows. East of the Cascade crest in Oregon and Washington, yields of grand or white fir stands at age 100 years range from 476 to 1330 m^3/ha (6,800 to 19,000 ft^3/acre) *(4)*. In northern Idaho, where grand fir grows with western white pine, predicted yields of normal stands range from 470 to 1078 m^3/ha (6,720 to 15,400 ft^3/acre) at age 100 *(14)*. Estimates of mean annual growth range from 8 to 13 m^3/ha (114 to 186 ft^3/acre) in Idaho *(27)* and 6 to 10 m^3/ha (86 to 143 ft^3/acre) in Montana *(23)*. On the more fertile soils of England, growth rates of 18 to 20 m^3/ha (257 to 286 ft^3/acre) to age 40 have been reported *(2)*.

Rooting Habit—The grand fir root system is intermediate in development among its associated tree species. The anchoring taproot does not grow as rapidly nor as deeply as dry site associates such as ponderosa pine, Douglas-fir, and lodgepole pine, but it grows faster and deeper than wet site species such as western hemlock, western redcedar, and Engelmann spruce. Seedling roots penetrate the soil rapidly enough in full sunlight to survive drought conditions in duff and surface soil. Grand fir produces roots under shaded conditions, enabling it to survive in the understory. The adaptable root system contributes to the growth of grand fir over a wide range of sites and climatic conditions. A relatively deep taproot enables grand fir to survive and grow well on rather dry soils and exposed ridges. On moist sites, the taproot is largely replaced by more shallow lateral roots *(9)*.

Reaction to Competition—Grand fir is classed as shade-tolerant in all associations in which it occurs. In the Willamette Valley of Oregon, it is the climax type following Douglas-fir and Oregon white oak. In the Inland Empire it is more tolerant than any of its associates except western redcedar and western hemlock. It is the climax type on sites too dry for redcedar or hemlock. In coastal British Columbia, grand fir is similar to Sitka spruce in tolerance; that is, it is slightly more tolerant than Douglas-fir. It is the least shade-tolerant of the true firs in British Columbia and is much less tolerant than western hemlock, western redcedar, or Pacific silver fir. Grand fir is a versatile species that, although quite tolerant, has a growth rate nearly equal to that of western white pine.

Grand fir is a dominant climax species in some habitat types and a long-lived seral species in other types. It usually grows in mixed-species stands where either even-aged or uneven-aged silviculture is practiced. In the zone of genetic intergrade between grand and white fir, it is not possible to separate the two species and their hybrids visually. Silvicultural prescriptions and treatments are applied as if they were one species. Where grand fir is desired under even-aged management, shelterwood cuttings are preferred because regeneration and early growth are best in partial shade. It also regenerates satisfactorily on most sites, however, following seed tree or clearcutting *(3,24)*. Following seedling establishment, the overstory should be removed to encourage rapid growth in height and diameter.

Under uneven-aged management, grand fir regenerates adequately and commonly outgrows the more tolerant western hemlock and western redcedar as an understory tree. Certain classes of understory grand fir saplings respond positively to release while others respond negatively *(8,25)*. Pole-size and larger grand firs respond well to release by thinning and selection cuttings if the crowns are vigorous *(13)*.

Damaging Agents—During the period of stand development from establishment to maturity, several factors influence stand growth and yield. Grand fir is rated medium in fire resistance among species of the western white pine type; it is less resistant than thick-barked western larch, ponderosa pine, and Douglas-fir but more resistant than subalpine fir, western hemlock, and Engelmann spruce. Fire resistance is influenced by habitat. For example, in moist creek bottoms grand fir succumbs rapidly to ground fires, but on dry hillsides it is more resistant, largely because of its deeper root system and thicker bark. The needles are quite resistant to cold during the severest part of the winter. Grand fir leaves have been subjected to temperatures of -55° C (-67° F) without damage. Sudden extreme drops of temperature in the fall occasionally damage needles, but seldom are they fatal. Frost cracks and lightning scars appear more frequently on grand fir, however, than on its associates in the Inland Empire. The cracks cause little direct mortality but contribute to the spread of infection by decay fungi. Often small patches of trees are uprooted or broken by the accumulation of snow in the crowns of dense immature stands in the Inland Empire *(9)*. In England young grand firs from Vancouver Island and western Washington are reportedly susceptible to late spring frost and drought crack *(2)*.

Susceptibility to heart rot and decay is one of the more important factors in the management of grand fir. Indian paint fungus *(Echinodontium tinctorium)* is the most destructive fungus in forests east of the Cascade crest *(17)*. In the Blue Mountains of Oregon and Washington, decay was reported responsible for losses of 14 percent of the gross merchantable cubic-foot volume and 33 percent of the board-foot volume in sawtimber-size grand fir trees *(1)*. Fungi enter the tree through small shade-killed branchlets in the lower crown. After closure of the branchlet stub, infections become dormant. Years later the infections are reactivated when mechanical injuries allow air to enter the heartwood where the dormant infections are located *(7)*. Therefore, centers of decay are closely related to logging scars, frost cracks, broken tops, and other mechanical injuries *(21)*.

Indian paint fungus is rare in grand fir west of the Cascade crest where rapid growth rates close branch stubs quickly *(7)*. *Armillaria* spp. and *Phellinus weiri* are the two most important root rot fungi. *Poria subacida* and *Heterobasidion annosum* also attack grand fir *(17)*.

Numerous insects attack grand fir. The western spruce budworm *(Choristoneura occidentalis)* and Douglas-fir tussock moth *(Orgyia pseudotsugata)* have caused widespread defoliation, top kill, and mortality. The western balsam bark beetle *(Dryocoetes confusus)* and the fir engraver *(Scolytus* *ventralis)* are the principal bark beetles attacking grand fir. The fir cone moth *(Barbara* spp.), fir cone maggots *(Earomyia* spp.), and several seed chalcids destroy large numbers of grand fir cones and seeds. The balsam woolly adelgid *(Adelges piceae)*, often called "gout disease of fir," has destroyed grand fir in western Oregon and Washington and is a serious threat in southwestern British Columbia *(12)*.

Special Uses

The soft white wood of grand fir is a valued source of pulpwood. The wood also is commercially valuable as timber even though it is weaker and more prone to decay than many other species. The luxuriant foliage, symmetry, and deep green shiny color make grand fir one of the preferred species of Christmas trees grown in the Northwest. The attractive appearance of grand fir makes it valuable in recreation areas and urban plantings.

Genetics

Population Differences

There are no *recognized* varieties of grand fir, although a green coastal form and gray interior form are often recognized. Five fairly distinct climatic forms of grand fir have been identified. The differences are mainly physiological and ecological *(9)*. Provenance trials with grand fir in Europe have resulted in ranking U.S. seed origins. Seed sources west of the Cascade crest are preferred for planting in England and the lowland sites in Europe *(20)*. Significant differences in height growth between trees from sources east and west of the Cascade crest have been reported but average growth of westside and interior seedlings is generally about the same *(29)*. Most of the genetic variation available for tree improvement appears to be among stands but genetic gains can also be made by selecting individuals within stands.

Hybrids

Grand fir crosses with both the *concolor* and *lowiana* varieties of white fir. Several studies have shown hybridization and introgression between grand fir and white fir in a broad zone extending from the Klamath Mountains of northern California through southwestern Oregon and through the Oregon Cascade Range into northeastern Oregon and west-central Idaho *(30)*. Grand fir has been crossed with several European and Asiatic species *(19)*. Natural hybrids have been reported between grand fir and subalpine fir in northern Idaho *(6)*.

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Abies lasiocarpa (Hook.) Nutt. Subapline Fir

Pinaceae Pine family

Robert R. Alexander, Raymond C. Shearer, and Wayne D. Shepperd

Subalpine fir, the smallest of eight species of true fir indigenous to the western United States, is distinguished by the long, narrow conical crown terminating in a conspicuous spikelike point (fig. 1).

Two varieties are recognized: the typical variety (*Abies lasiocarpa* var. *lasiocarpa*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*). The latter, readily distinguished by its peculiar, whitish, corky bark, is restricted to the Rocky Mountains of southern Colorado and the Southwest. Other common names for the typical variety include balsam, white balsam, alpine fir, western balsam fir, balsam fir, Rocky Mountain fir, white fir, and pino real blanco de las sierras; for corkbark fir, alamo de la sierra *(44)*.

Habitat

Native Range

Subalpine fir is a widely distributed North American fir (fig. 2). Its range extends from 32° N. latitude in Arizona and New Mexico to 64° 30 N. in Yukon Territory, Canada. Along the Pacific coast, the range extends from southeastern Alaska, south of the Copper River Valley (lat. 62° N.), the northwestern limit; east to central Yukon Territory (lat. 64° 30′ N.), the northern limit; south through British Columbia along the east slopes of the Coast Range to the Olympic Mountains of Washington, and along both slopes of the Cascades to southern Oregon. It is not found on the west slopes of the Coast Range in southern British Columbia or along the Coast Range in Washington and Oregon, but it does occur on Vancouver Island *(2,9)*. It is also found locally in northeastern Nevada and northwestern California *(43)*. Except where noted above, subalpine fir is a major component of high elevation Pacific Northwest forests.

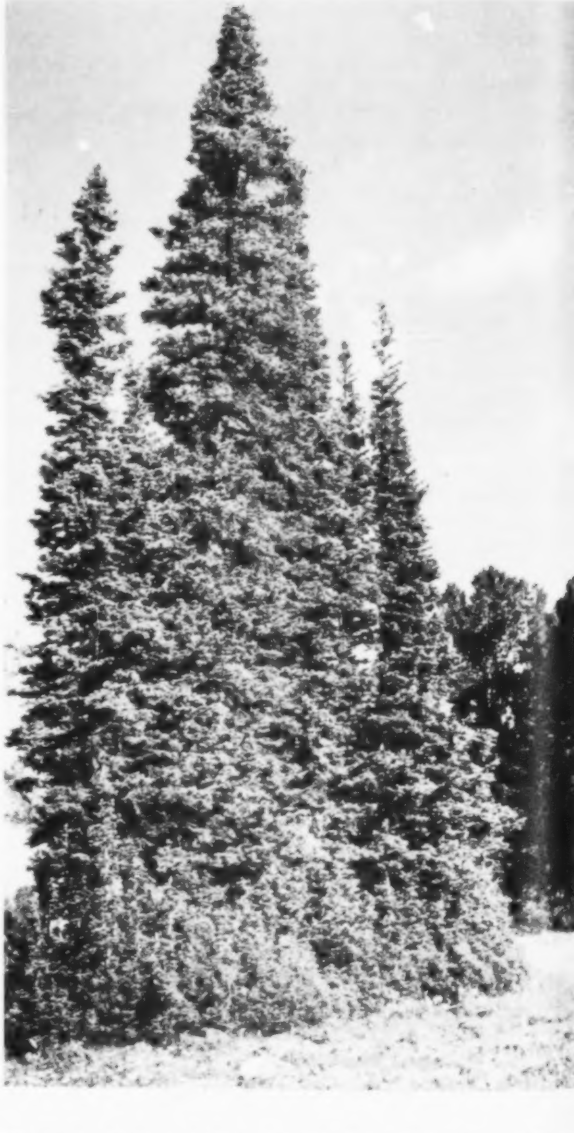

Figure 1—*Mature subalpine fir on the Fraser Experimental Forest Colorado.*

In the Rocky Mountain region, subalpine fir extends from the interior valleys of British Columbia west of the Continental Divide and south of the Peace River (lat. 55° N.), south along the high elevations of the Rocky Mountain system to southern New Mexico and Arizona. In the north, its range extends from the high mountains of central British Columbia, western Alberta, northeastern Washington, northeastern Oregon, Idaho, Montana, to the Wind River Mountains of western Wyoming. In Utah, it commonly occurs in the Uinta and Wasatch Mountains, but is less abundant on the southern plateaus. The range extends from southern Wyoming, through the high

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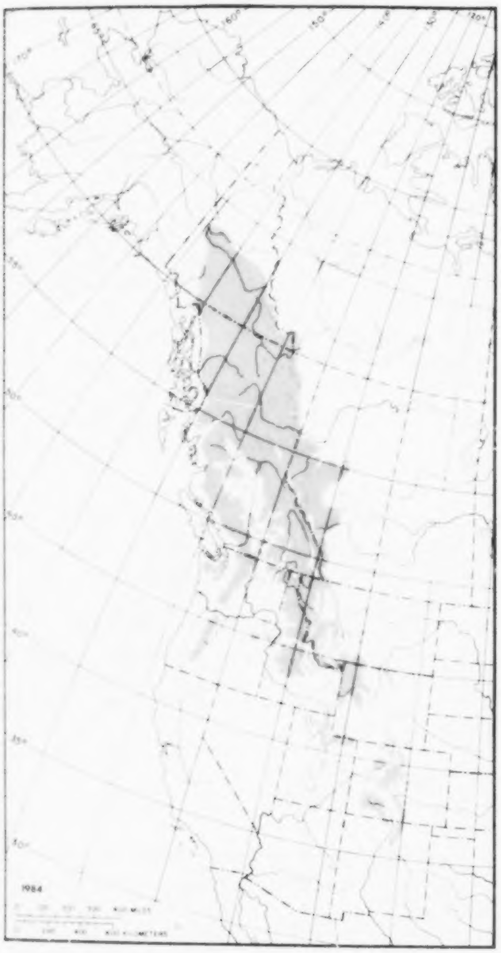

Figure 2—*Natural range of subalpine fir (Abies lasiocarpa).*

mountains of Colorado and northern New Mexico, and westward through northeastern Arizona to the San Francisco Mountains *(2,9)*. Subalpine fir is a major component of the high-elevation forests of the Rocky Mountains.

Corkbark fir is found mixed with subalpine fir on scattered mountains in southwestern Colorado; northern, western, and southwestern New Mexico; and in the high mountains of Arizona *(44)*.

Climate

Subalpine fir grows in the coolest and wettest forested continental area of western United States *(58)*. Temperatures range from below -45° C (-50° F) in the winter to more than 32.2° C (90° F) in the summer. Although widely distributed, subalpine fir grows within a narrow range of mean temperatures. Mean annual temperatures vary from -3.9° C (25° F) to 4.4° C (40° F), with a July mean of 7.2° C to 15.6° C (45° F to 60° F), and a January mean of -15.0° C to -3.9° C (5° F to 25° F) *(10,26,47)* (table 1). Average precipitation exceeds 61 cm (24 in), much of which falls as snow. More than half the precipitation occurs from late fall to late winter in the Pacific Northwest and west of the Continental Divide in the Rocky Mountains north of Utah and Wyoming. East of the Divide, in the Rocky Mountains north of New Mexico and Arizona, the heaviest precipitation comes in late winter and early spring. In the Rocky Mountains and associated ranges in Arizona and New Mexico, most precipitation comes during late summer and early fall *(5,10,58)*. However, cool summers, cold winters, and deep winter snowpacks are more important than total precipitation in differentiating where subalpine fir grows in relation to other species.

Soils and Topography

Information on soils where subalpine fir grows is limited. In the Pacific Coast region, soil parent materials are mixed and varied. Zonal soils in the subalpine fir zone are Cryorthods (Podzolic soils), or Haplorthods (Brown Podzolic soils) with well developed but ultimately thin humus layers. Haploxerults and Haplohumults (Reddish-Brown Lateritic soils), developed from volcanic lava; Xerochrepts (Regosolic soils), developed from shallow residual material; and Lithic (Lithosolic soils) are also common in some localities. Dystrandepts (Bog soils) and Haplaquepts (Humic Gley soils) occur on poorly drained sites. Soils are more acid than in lower elevation forests, with pH typically ranging from 4.5 to 5.9 *(22,61)*.

In the central and southern Rocky Mountains subalpine zone, soil materials vary according to the character of the bedrock from which they originated. Crystalline granite rock predominates, but conglomerates, shales, sandstones, basalts, and andesites commonly occur. Glacial deposits and stream alluvial fans are also common along valley bottoms. Of the great soils group, Cryorthods (Podzolic Soils) and Haplorthods (Brown Podzolic Soils) occur extensively on all aspects. Cryochrepts (Sols Bruns Acides) occur extensively on the drier aspects. Aquods (Ground-Water Podzolic Soils) are found in the more poorly drained areas. Cryoboralfs (Gray-Wooded Soils) have fine-textured parent material and support low-density timber stands. Haploboralls (Brown Forest Soils) occur mostly in the lower subalpine zone along stream terraces and side slopes. Lithics (Lithosolic Soils) occur whenever bedrock is near the

Table 1—Climatological data for four regional subdivisions within the range of subalpine fir.

Location	Average temperature						Annual precip.		Annual snowfall		Frost each period
	Annual		July		January						
	°C	°F	°C	°F	°C	°F	*cm*	*in*	*cm*	*in*	*days*
Pacific Northwest	−1 to 4	30–35	7–13	45–55	−9 to −4	15–25	61–254+	24–100+	1524+	600+	30–60
U.S. Rocky Mountains											
Northern[1]	−4 to 2	25–35	7–13	45–55	−15 to −9	5–15	61–152	24–60	635+	250+	30[4]–60
Central[2]	−1 to 2	30–35	10–13	50–55	−12 to −9	10–15	61–140	24–55	381-889+	150–350+	30[4]–60
Southern[3]	−1 to 4	30–40	10–16	50–60	−9 to −7	15–20	61–102+	24–40+	508	200+	30[4]–75

[1] Includes the Rocky Mountains north of Wyoming and Utah, and associated ranges in eastern Washington and Oregon.
[2] Includes the Rocky Mountains of Colorado, Wyoming and Utah.
[3] Includes the Rocky Mountains and associated ranges of New Mexico and Arizona, and the plateaus of southern Utah.
[4] Frost may occur any month of the year.

surface. Aquepts (Bog Soils) and Haplaquepts (Humic Gley Soils) occur extensively in poorly drained upper stream valleys *(31,61)*.

Regardless of the great soils groups that occur in the subalpine zone of the west, subalpine fir is not exacting in its soil requirements. It is frequently found growing on soils that are too wet or too dry for its common associates. Good growth is made on lower slopes, alluvial floodplains, and glacial moraines; and at high elevations on well drained, fine- to medium-textured sand and silt loams that developed primarily from basalt, andesite, and shale. Growth is poor on shallow and coarse-textured soils developed from granitic and schistic rock, conglomerates, and coarse sandstones, and on saturated soils, but subalpine fir establishes on severe sites, such as lava beds, tallus slopes, and avalanche tracks, before any of its common associates. Under these conditions it may pioneer the site for other species or it may exclude the establishment of other species *(9,23)*.

Subalpine fir grows near sea level at the northern limit of its range, and as high as 3658 m (12,000 ft) in the south. In the Coast Range of southeastern Alaska, it is found from sea level to 1067 m (3,500 ft); in the Coast Range and interior plateaus of Yukon Territory and British Columbia, at 610 to 1524 m (2,000 to 5,000 ft); and in the Olympic and Cascade Mountains of Washington and Oregon, generally at 1219 to 1829 m (4,000 to 6,000 ft), but as low as 610 m (2,000 ft) along cold stream bottoms and on lava flows, and as high as 2438 m (8,000 ft) on sheltered slopes *(9,57)*.

In the Rocky Mountains of British Columbia and Alberta south of the Peace River, subalpine fir grows at 914 to 2134 m (3,000 to 7,000 ft), but it is more abundant above 1524 m (5,000 ft); in the Rocky Mountains of Montana and Idaho and associated ranges in eastern Washington and Oregon, at 610 to 3353 m (2,000 to 11,000 ft), but it is more common at 1524 to 2743 m (5,000 to 9,000 ft) *(40,41)*; in the Rocky Mountains of Wyoming, Utah, and Colorado, usually at 2743 to 3353 m (9,000 to 11,000 ft), but it may be found as low as 2438 m (8,000 ft) and to timberline at 3505 m (11,500 ft); and in the Rocky Mountains and associated ranges of New Mexico and Arizona, at 2438 to 3658 m (8,000 to 12,000 ft), but usually on north slopes at 2896 to 3353 m (9,500 to 11,000 ft) *(9,12,46,52)*.

Associated Forest Cover

In the Rocky Mountains, subalpine fir is most typically found in mixture with Engelmann spruce (*Picea engelmannii*) and forms the relatively stable Engelmann Spruce—Subalpine Fir (Type 206) forest cover type. It is also found in varying degrees in 16 other cover types *(56)*:

SAF Type No.	Type Name
201	White Spruce
202	White Spruce—Paper Birch
205	Mountain Hemlock
208	Whitebark Pine
209	Bristlecone Pine
210	Interior Douglas-Fir
212	Western Larch
213	Grand Fir
215	Western White Pine
216	Blue Spruce
217	Aspen
218	Lodgepole Pine
219	Limber Pine
223	Sitka Spruce
224	Western Hemlock
226	Coastal True Fir--Hemlock

Differences in elevation and latitude affect temperature and precipitation, influencing the composition of the forests where subalpine fir grows *(16)*.[1] In Alaska and the Coast Range of British Columbia south through the Coast Range of Washington and Oregon, mountain hemlock *(Tsuga mertensiana)* is its common associate. In Alaska and northern British Columbia, Alaska-cedar *(Chamaecyparis nootkatensis)* mixes with it; and where it approaches sea level, it mingles with Sitka spruce *(Picea sitchensis)*. From southern British Columbia southward through much of the Cascades, Pacific silver fir *(Abies amabilis)*, mountain hemlock, and lodgepole pine *(Pinus contorta)* are the most common associates under closed forest conditions. Major timberline associates are mountain hemlock and whitebark pine *(Pinus albicaulis)*. Engelmann spruce is not a constant associate of subalpine fir except on the east slopes of the northern Cascades, and on exceptionally moist, cool habitats scattered throughout the southern and western Cascades. Engelmann spruce is a major associate of subalpine fir in the mountains of eastern Washington and Oregon. Less common associates in the Pacific Northwest include western hemlock, noble fir *(Abies procera)*, grand fir *(Abies grandis)*, western white pine *(Pinus monticola)*, western larch *(Larix occidentalis)*, and alpine larch *(Larix lyallii) (2,9)*.

From the mountains and interior plateaus of central British Columbia southward through the Rocky Mountain system, where subalpine fir frequently extends to timberline, its most constant associate is Engelmann spruce. Less common associates include: in British Columbia and western Alberta, white spruce *(Picea glauca)*, balsam poplar *(Populus balsamifera)*, paper birch *(Betula papyrifera)*, and aspen *(Populus tremuloides)*; in the Rocky Mountains of Montana and Idaho at its lower limits, western white pine, interior Douglas-fir *(Pseudotsuga menziesii* var. *glauca)*, western hemlock *(Tsuga heterophylla)*, western larch, grand fir, and western redcedar *(Thuja plicata)*; and at higher elevations, lodgepole pine, alpine larch, mountain hemlock, and whitebark pine. In the Rocky Mountains of Wyoming, Utah, and Colorado, near its lower limits, associates are lodgepole pine, interior Douglas-fir, aspen, and blue spruce *(Picea pungens)*; and at higher elevations, whitebark pine, limber pine *(Pinus flexilis)*, and bristlecone pine *(Pinus aristata)*; and in the Rocky Mountains and associated ranges of New Mexico and Arizona, near its lower limits, white fir *(Abies concolor)*, interior Douglas-fir, blue spruce, and aspen; and at higher elevations, corkbark fir. Subalpine fir frequently extends to timberline in the Rocky Mountains. Other species that accompany it to timberline are whitebark pine, mountain hemlock, and occasionally Engelmann spruce in the Rocky Mountains north of Utah and Wyoming; Engelmann spruce in the Rocky Mountains north of Wyoming, Utah, and Colorado; and Engelmann spruce and corkbark fir in the Rocky Mountains and associated ranges south of Wyoming and Utah *(2,9)*.

At timberline in the Rocky Mountains, subalpine fir and Engelmann spruce form a wind Krummholz 1 to 2 m (3 to 7 ft) high. On gentle slopes below timberline, subalpine fir, Engelmann spruce, and occasionally lodgepole pine grow in north-south strips 10 to 50 m (33 to 164 ft) wide and several hundred meters long approximately at right angles to the direction of prevailing winds. These strips are separated by moist subalpine meadows 25 to 75 m (82 to 246 ft) wide where deep snow drifts accumulate *(14)*.

Undergrowth vegetation is more variable than tree associates. In the Pacific Northwest and the Rocky Mountains and associated ranges north of Utah and Wyoming, common undergrowth species include: Labrador tea *(Ledum glandulosum)*, Cascades azalea *(Rhododendron albiflorum)*, rusty skunkbrush *(Menziesia ferruginea)*, woodrush *(Luzula hitchcockii)*, Rocky Mountain maple *(Acer glabrum)*, twinflower *(Linnaea borealis)*, dwarf huckelberry *(Vaccinium caespitosum)* and blue huckleberry *(V. globulare)* (cool, moist sites); queens cup *(Clintonia uniflora)*, twistedstalk *(Streptopus amplexiflolius)*, and sweetscented bedstraw *(Galium triflorum)* (warm, moist sites); grouse whortleberry *(V. scoparium)*, fireweed *(Epilobium angustifolium)*, mountain gooseberry *(Ribes montigenum)*, heartleaf arnica *(Arnica cordifolia)*, beargrass *(Xerophyllum tenax)*, boxleaf myrtle *(Pachystima myrsinites)*, elksedge *(Carex geyeri)*, and pine grass *(Calamagrostis rubescens* (cool, dry sites); creeping juniper *(Juniperus communis)*, white spirea *(Spiraea betulaefolia)*, Oregongrape *(Berberis repens)*, a mountain snowberry *(Symphoricarpos oreophilus)*, and big whortleberry *(V. membranaceum)* (warm, dry sites); and marsh-marigold *(Caltha biflora)*, devilsclub *(Oplopanax horrida)*, and bluejoint reedgrass *(Calamagrostis canadensis)* (wet sites) *(6,22)*.

Undergrowth characteristically found in the Rocky Mountains and associated ranges south of Idaho and Montana includes: mountain bluebells *(Mertensia ciliata)* and heartleaf bittercress *(Cardamine cordifolia)* (cool, moist sites); thimbleberry *(Rubus parviflorus)* (warm, moist sites); red buffaloberry

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[1] Classification of forest vegetation into "habitat types" based on the methodology developed by Daubenmire *(17)* and Daubenmire and Daubenmire *(18)*, and modified by others, is available for much of the western forest land. However, the classification has not been completed for all land where subalpine fir grows. Moreover, because of the great number of these habitat types and the complexity of their descriptions, they have not been included in this paper

(Shepherdia canadensis), Oregongrape, creeping juniper, mountain snowberry (warm, dry sites); and Rocky Mountain whortleberry *(V. myrtillus)*, grouse whortleberry, fireweed, heartleaf arnica, groundsel *(Senecio sanguiosboides)*, polemonium *(Polemonium delicatum)*, daisy fleabane *(Erigeron eximius)*, elksedge, boxleaf myrtle, prickly currant *(Ribes lacustre)*, sidebells pyrola *(Pyrola secunda)*, and mosses (cool, dry sites) *(6)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Subalpine fir flowers are monoecious. Male flowers, usually abundant, are borne in pendulous clusters from the axils of the needles on the lower branchlets. Female flowers are fewer, borne erect and singly on the uppermost branchlets of the crown. Male flowers ripen, and pollen is wind-disseminated, during late spring and early summer. Cones are indigo blue when they open in mid-August to mid-October. Seed ripens from mid-September to late-October *(45,60)*.

Seed Production and Dissemination—Subalpine fir may begin to produce cones when trees are 1.2 to 1.5 m (4 to 5 ft) tall and 20 years old, but under closed-forest conditions, seed production is not significant until trees are older and taller. Corkbark fir does not begin to bear cones until about 50 years old. Maximum seed production for subalpine and corkbark fir occurs in dominant trees 150 to 200 years old *(9,60)*.

Subalpine fir is a good seed producer in the Pacific Northwest and in the Rocky Mountains of Idaho and Montana, with good to heavy crops borne every 3 years, and light crops or failures in between *(24,42)*. It is as good a seed producer as most associated true firs, but not as good as the hemlocks and Engelmann spruce. In one 11-year study at four locations in the Cascades, subalpine fir cone crops, based on the following criteria, were rated medium to very heavy in 6 years and very light to failure in the other 5 *(24)*.

Number of cones/tree	Crop rating
0	Failure
1-9	Very light
10-19	Light
20-49	Medium
50-99	Heavy
100+	Very heavy

In the Rocky Mountains south of Idaho and Montana, seed production of subalpine and corkbark fir has generally been poor, with more failures than good seed years. In one study in Colorado covering 42 area-seed-crop years, subalpine fir was an infrequent seed producer. Some seed was produced in only 8 of the years, while the other 34 were complete failures *(50)*. Similar results have been obtained from other seed-production studies in Colorado. However, because these studies were designed to sample seed production in spruce-fir stands and because Engelmann spruce made up 90 percent or more of the dominant stand basal area, these results only indicate subalpine fir seed production in spruce-fir stands, not of individual dominant fir trees *(9)*.

A number of cone and seed insects of subalpine fir have been identified but their relative importance, frequency of occurrence, and the magnitude of losses are not known *(39)*. Some seed is lost from cutting and storing of cones by pine squirrels *(Tamiasciurus hudsonicus fremonti)*, and, after seed is shed, small mammals, such as deer mice *(Clethrionomys gapperi)*, mountain voles *(Microtus montanus)*, and western chipmunks *(Eutamias minimus)*, consume some seeds *(5)*. However, the amount of seed lost to mammals, birds, and other causes are not known.

Cones disintegrate when they are ripe. Scales fall away with the large, winged seeds, leaving only a central, spikelike axis. Dissemination beginning in September usually is completed by the end of October in the Rocky Mountains. In the Pacific Northwest, seed dissemination begins in October and usually continues into November, but pitched-up cones may extend dissemination into December. Nearly all seed is dispersed by the wind *(21,60)*.

Subalpine fir seeds are fairly large, averaging 76,720/kg (34,800/lb). Little information is available on seed dispersal distances. Studies designed to measure Engelmann spruce seed dispersal show similar dispersal patterns for subalpine fir. Prevailing winds influence the dispersal pattern, with about half the seeds falling into openings within 30 m (100 ft) of the windward timber edge. Seedfall continues to diminish until about two-thirds the way across the opening, and then levels off before slightly increasing about 15 m (50 ft) from the leeward timber edge *(50)*. Thermal upslope winds are important in seed dispersal in mountainous terrain at mid- to lower-elevations *(54)*.

Subalpine fir seed viability is only fair: average germinative capacity is 34 percent and vitality transient *(60)*. Observations and limited studies in the Rocky Mountains indicate that germinative capacity is often less than 30 percent *(55)*. Some lots of stored seeds exhibit embryo dormancy, which can be broken by stratification in moist sand or peat at 5° C (41° F) for 60 days *(9,60)*.

Seedling Development—Under natural conditions, fir seeds lie dormant under the snow and germinate the following spring. Although germination and early survival of subalpine fir are generally best on exposed mineral soil and moist humus, the species is less exacting in its seedbed requirements than most of its common associates. Subalpine fir has been observed to germinate and survive on a wide variety of other seedbed types including the undisturbed forest floor, undecomposed duff and litter, and decaying wood *(9,15,19)*. Subalpine fir also invades and establishes on severe sites such as recent burns, lava flows, talus slopes, avalanche tracks, and climatically severe regions near timberline *(22)*. Subalpine fir succeeds on these open sites because of its ability to establish a root system under conditions too severe for its less hardy associates, and its ability to reproduce by layering.

Although subalpine fir grows under nearly all light intensities found in nature, establishment and early survival are usually favored by shade. In the absence of Pacific silver fir, grand fir, and mountain hemlock, subalpine fir will survive under closed-forest conditions with less light than Engelmann spruce, noble fir, and white spruce *(22)*. When grown with Pacific silver and grand fir, and/or mountain hemlock, subalpine fir does not compete successfully under closed-forest conditions. It does not compete well with the spruces, lodgepole pine, or interior Douglas-fir when light intensity exceeds 50 percent of full shade *(9)*.

Subalpine fir is restricted to cold, humid habitats because of low tolerance to high temperatures. Newly germinated subalpine fir seedlings tolerate high solar radiation, but they are susceptible to heat girdling and drought. Seedlings are also killed or damaged by spring frosts, competing vegetation, frost heaving, damping off, snowmold, birds, rodents, and trampling and browsing by large animals, but losses are not different than for any common associate *(5)*.

The number of seeds required to produce a first-year seedling, and an established seedling (at least 3 years old), and the number of first-year seedlings that produce an established seedling vary considerably, depending upon seed production, distance from source, seedbed, and other environmental conditions. In one study in Colorado, covering the period 1961 to 1975 and a wide variety of conditions, an average of 150 seeds (range 35 to 290) was required to produce a first-year seedling. An average of 755 seeds (range 483 to 1,016) was required to produce a 4- to 13-year-old established seedling. For every established 4- to 13-year-old seedling, an average of 10 first-year seedlings were required, with a range of as few as 4 to as many as 14 *(50)*.

Early root growth of subalpine fir is very slow. The root length of first-year seedlings in one study in British Columbia averaged only 6.8 cm (2.7 in) *(20)*. No comparable data are available in the United States, but first-year penetration of corkbark fir in Arizona averaged 8.6 cm (3.4 in) *(32)*.

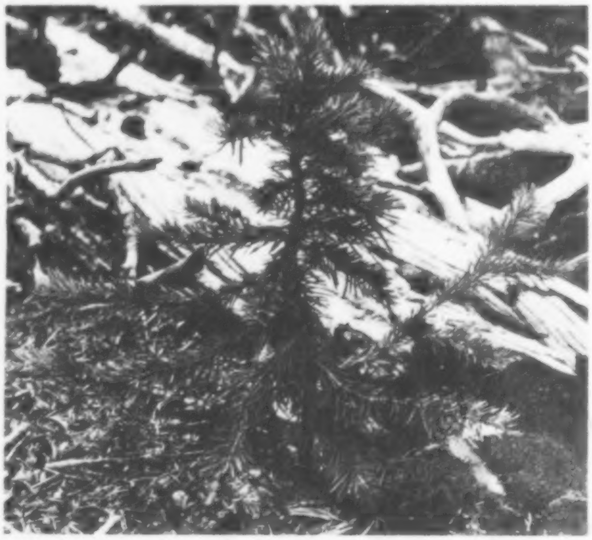

Figure 3—*Subalpine fir seedlings average less than 38 cm (15 in) in height after 15 years in the open.*

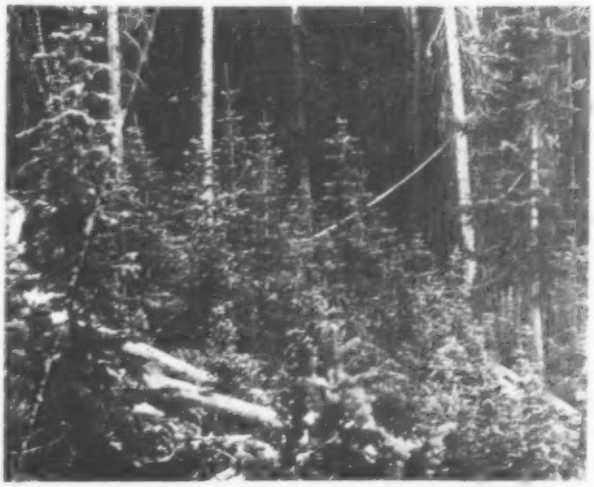

Figure 4—*Subalpine fir advanced reproduction released by removal of the overstory. Trees averaged 1.0 to 1.8 m (3 to 6 ft) in height and are at least 50 years old.*

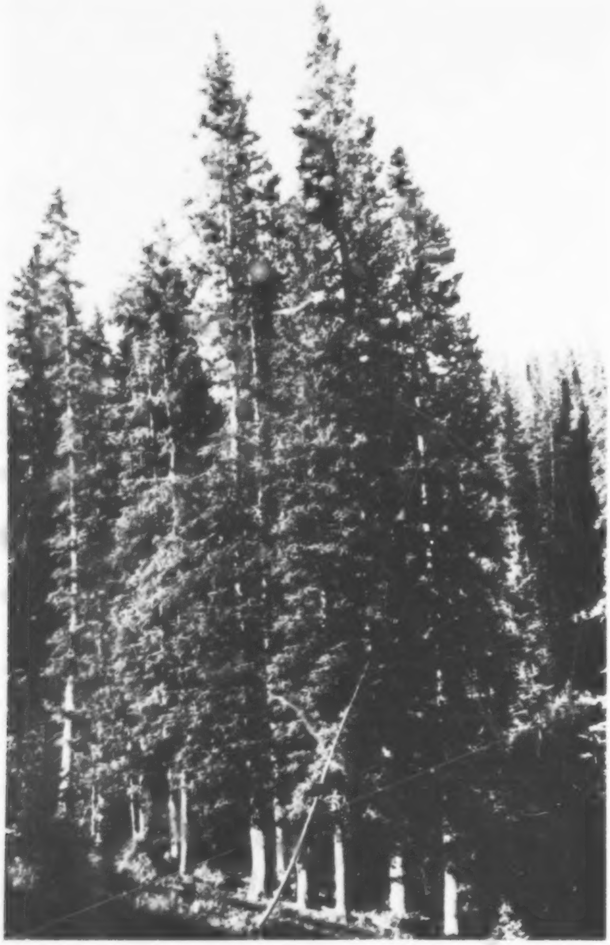

Figure 5—*Dominant subalpine firs on the Fraser Experiment Forest, Colorado. These trees are about 30 to 35 cm (12 to 14 in) in diameter, about 18 m (60 ft) tall, and over 200 years old at breast height.*

Shoot growth is equally slow at high elevations. Many first-year seedlings are less than 2.5 cm (1 in) tall. Annual height growth of seedlings during the first 10-15 years usually averages less than 2.5 cm (1 in) (fig. 3).

In one study, seedlings 15 years old averaged only 28 cm (11 in) in height on burned-over slopes, 25 cm (10 in) on cutover, dry slopes, and 15 cm (6 in) on cutover, wet flats *(30)*. In another study, seedlings grown on mineral soil averaged only 58.8 cm (24 in) after 21 years *(28)*. Trees reach 1.2 to 1.5 m (4 to 5 ft) in height in 20 to 40 years under favorable environmental conditions. However, trees less than 13 cm (5 in) in diameter are often 100 or more years old at higher elevations, and trees 1.2 to 1.8 m (4 to 6 ft) high and 35 to 50 years old are common under closed-forest conditions *(40,51)* (fig. 4).

At lower elevations, seedling shoot growth has been better. In one study in the Intermountain West, average annual height growth of subalpine fir seedlings for the first 10-years after release was 11.4 cm (4.5 in) on clearcuts and 8.1 cm (3.2 in) on partial cuts *(48)*.

Vegetative Reproduction—Subalpine fir frequently reproduces by layering where the species is a pioneer in developing forest cover on severe sites such as lava flows and talus slopes or near timberline *(22)*. Under closed-forest conditions, reproduction by layering is of minor importance.

Sapling and Pole Stage to Maturity

Growth and Yield—On exposed sites near timberline, subalpine fir is often reduced to a prostrate shrub, but under closed-forest conditions it attains diameters of 30 to 61 cm (12 to 24 in) and heights of 14 to 30 m (45 to 100 ft), depending upon site quality and stand density (fig. 5). Trees larger than 76 cm (30 in) in diameter and 39.6 m (130 ft) in height are exceptional *(57)*.

Growth is not rapid; trees 25 to 51 cm (10 to 20 in) in diameter are often 150 to 200 years old under closed-forest conditions. Trees older than 250 years are not uncommon. But, because the species suffers severely from heartrot, many trees either die or are complete culls at an early age. Few data are available on the yields of subalpine fir in natural stands. It usually grows in mixed stands and comprises only a minor part of the volume. In the Rocky Mountains and Pacific Northwest, where it grows in association with Engelmann spruce, subalpine fir usually makes up only 10 to 20 percent of the saw log volume, which may range from less than 12,350 to more than 98,800 fbm/ha (5,000 to 40,000 fbm/acre) *(30,49)*. In the Pacific Northwest and Rocky Mountains, where subalpine fir grows with other true firs and/or mountain hemlock, few trees reach minimum merchantable size before being crowded out of the stand *(22)*. Subalpine fir in the Rocky Mountains grows in pure stands most often on sites so severe that it has little commercial value. In the Pacific Northwest, pure stands on commercial sites typically occur on southerly slopes and are usually less than 150 years old. These stands are not extensive but are distinctive *(21)*.

Managed Stands

The only data available for yields of subalpine fir in managed stands are estimated from simulations for mixed Engelmann spruce—subalpine fir stands in the Rocky Mountains south of Idaho and Montana *(7)*. These simulations show that periodic thinning to control stand density and maintain growth rates increases the yield and size of individual fir trees in these mixed stands. Furthermore, the growth rates for fir are similar to those for spruce early in the life of the stand. However, the fir component is likely to be greatly reduced by repeated thinnings, so that the stand at the time of final harvest will be almost pure Engelmann spruce.

Rooting Habit—Subalpine fir has a shallow root system on sites that limit the depth of root penetration, and where the superficial lateral root system common to the seedling stage persists to old age. Under more favorable conditions, subalpine fir develops a relatively deep lateral root system *(9)*.

Reaction to Competition—In the Rocky Mountains and Pacific Northwest where subalpine fir and Engelmann spruce form the spruce-fir type, and mountain hemlock and other true firs are absent or limited in number, subalpine fir is very shade-tolerant *(22)*. It is much more tolerant than spruce and other common associates such as lodgepole pine, aspen, blue spruce, and interior Douglas-fir *(11)*. However, in most of the Cascades and in the Rocky Mountains, where subalpine fir grows with the more shade-tolerant Pacific silver fir, grand fir, and mountain hemlock, some ecologists classify it as intolerant relative to these associates *(22)*.

Subalpine fir, together with Engelmann spruce, forms a climax or long-lived seral forest vegetation throughout much of its range. In the Rocky Mountains of British Columbia and Alberta and south of Montana and Idaho, subalpine fir and Engelmann spruce occur as either codominants or in pure stands of one or the other. Spruce, however, is most likely to form pure stands, especially at upper elevations. In the Rocky Mountains of Montana and Idaho and the mountains of eastern Oregon and Washington, subalpine fir is a major climax. Engelmann spruce may be either a major climax or a persistent long-lived seral. Pure stands of either species may occur, but subalpine fir is more likely to form pure stands, especially at high elevations *(2)*.

Although subalpine fir is a dominant element in several climax or near-climax vegetation associations, these forests differ from the typical climax forest in that most of them are not truly all-aged. For example, in spruce-fir forests, some stands are single-storied while others are two-, three-, and multi-storied. Multi-storied stands may result from past disturbances such as fire, insect epidemics, or cutting, or they may result from the gradual deterioration of single- and two-storied stands associated with normal mortality from wind, insects, and diseases *(5)*. On the other hand, some multi-storied stands appear to have originated as uneven-aged stands and are successfully perpetuating that structure *(3,27)*.

Where subalpine fir is a component of the climax vegetation, the natural tendency is for subalpine fir to reestablish itself when destroyed and temporarily replaced by other vegetation *(27)*. Throughout most of the Cascades and in the Rocky Mountains where subalpine fir grows with the other true firs and/or mountain hemlock, it is seral. Subalpine fir also is a pioneer on difficult sites, where its ability to reproduce by layering allows it to colonize more readily than its common associates *(22)*.

The ecophysiology of subalpine fir in relation to common associated species is becoming better understood *(33,34,35,36)*. What is known about the general water relations of subalpine fir can be summarized as follows: (1) needle water vapor conductance (directly proportional to stomatal opening) is controlled primarily by visible irradiance and absolute humidity difference from needle to air (evaporative demand) with secondary effects from temperature and water stress; (2) nighttime minimum temperatures below 3.9° C (39° F) retard stomatal opening the next day; (3) stomata function well from early spring to late fall, and high transpiration rates occur even with considerable snowpack on the ground; (4) leaf water vapor conductance is lower than that of Engelmann spruce, lodgepole pine, and aspen, the common associates of central Rocky Mountain subalpine forests; (5) subalpine fir trees have a larger total needle area per unit of sapwood water-conducting tissue than the other three species; and (6) subalpine fir trees have a slightly lower needle area per unit of bole or stand basal area than Engelmann spruce, but greater than lodgepole pine or aspen. At equal basal area, annual canopy transpiration of subalpine fir is about 35 percent lower than spruce, but 15 percent higher than lodgepole pine, and 100 percent higher than aspen. These high rates of transpiration cause subalpine fir to occur primarily on wet sites, generally in association with Engelmann spruce *(37,38)*.

Both even- and uneven-aged silvicultural systems can be used in stands where subalpine fir is a component *(1,5,8)*. The appropriate even-aged cutting methods are clearcutting and shelterwood cutting and their modifications. The seed-tree method cannot be used because of susceptibility of subalpine fir to windthrow. The uneven-aged cutting methods are individual tree and group selection and their modifications. In spruce-fir stands, shelterwood and individual-tree-selection methods will favor subalpine fir over Engelmann spruce, lodgepole pine, and interior Douglas-fir *(4)*. In stands where subalpine fir grows with Pacific silver fir, grand fir, and/or mountain hemlock, clearcutting and group shelterwood or group selection cutting will favor subalpine fir *(22)*.

Damaging Agents—Subalpine fir is susceptible to windthrow. Although, this tendency is generally attributed to a shallow root system, soil depth, drainage, and stand conditions influence the development of the root system. The kind and intensity of cutting and topographic exposure to wind also influence the likelihood of trees being windthrown *(5)*.

Subalpine fir is attacked by several insects *(39)*. In spruce-fir forests, the most important insect pests are the western spruce budworm *(Choristoneura occidentalis)* and western balsam bark beetle *(Dryocoetes confusus)*. The silver fir beetle *(Pseudohylesinus sericeus)* and the fir engraver *(Scolytus ventralis)* may at times be destructive locally *(25)*. In the Cascades, the balsam woolly adelgid *(Adelges piceae)*, introduced from Europe, is the most destructive insect pest. This insect has caused significant mortality to subalpine fir, virtually eliminating it from some stands in Oregon and southern Washington *(22)*.

Fir broom rust *(Melampsorella caryophyllacearum)* and wood rotting fungi are responsible for most disease losses *(13,29,53)*. Important root and butt rots are *Gloeocystidiellum citrinum, Coniophora puteana, Armillaria mellea, Coniophorella olivaea, Polyporus tomentosus* var. *circinatus,* and *Pholiota squarrose*. Important trunk rots are *Haematostereum sanguinolentum, Phellinus pini,* and *Amylostereum chailletii*. Wood rots and broom rust weaken affected trees and predispose them to windthrow and windbreak *(5)*.

Subalpine fir bark is thin, especially on young trees, and lower limbs persist after death *(9)*. These characteristics make subalpine fir susceptible to death or severe injury from fire.

Special Uses

Throughout much of the Rocky Mountains, subalpine fir has no special or unique properties. In the high Cascades and in the Rocky Mountains of Idaho and Montana, it is a forest pioneer on severe and disturbed sites. By providing cover, subalpine fir assists in protecting watersheds and rehabilitating the
landscape. Forests in which
cupy the highest water yiel
West.

The species also provides h
and nongame animals, forag
tional opportunities, and s
these properties are indigen
subalpine fir grows rather
properties associated with th

Fir is used as lumber in
boxes, crates, planing mill p
frames, and food containers.
used for pulpwood because
can be pulped readily by
groundwood processes *(59)*.

Genetics

Population Differences

Information on subalpine fi
is virtually nonexistent. Un
with the range in elevation a
fir will exhibit differences in
mancy, resistance to heat an
ferent populations.

Races and Hybrids

Corkbark fir is the onl
geographical variety of subalp
species with wide distribu
developed unknown races an
some evidence that natural i
tion between subalpine and b
they grow together in Canada
namental cultures have been
include:

1. *Abies lasiocarpa* cv *beiss*
ing distorted branches and tw
2. *A. l.* cv *coerulescens* a b
cially intensive bluish needles
3. *A. l.* cv *compacta*. A dwarf

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Abies magnifica A. Murr. California Red Fir

Pinaceae Pine family

Robert J. Laacke

Red fir (*Abies magnifica*) dominates large areas of high country that are a major source of water, especially in California. For this reason it has long been an important forest tree. Only recently has red fir assumed significance as an unusually productive source of wood ([illegible]). Relatively little detailed, [illegible] information is available, however.

North of Mount Lassen in northern California, red fir shows morphological and perhaps ecological characteristics that have led to its common designation as Shasta red fir (*A. magnifica* var. *shastensis*) ([illegible]). Here the varieties are referred to collectively as red fir and are identified only when differences warrant.

Habitat

Native Range

[illegible]

[illegible] Cascade and Siskiyou Mountains [illegible] toward the south, reaching to [illegible] in the southern Sierra Nevada. Upper elevation limits also increase to the south, beginning at 2010 to 2190 m (6,600 to 7,200 ft) in the Cascade and Siskiyou Mountains, and reaching 2740 m (9,000 ft) in the southern Sierra Nevada. Red fir can be found growing at lower elevations in canyons and other protected places where significant cold air drainage keeps soil and air temperatures low (37). In the California Coast Ranges, Shasta red fir is found generally between 1400 and 1830 m (4,600 to 6,000 ft) (8,9,33).

Climate

Climate for the red fir zone can be classified in general as cool and moist to cold and moist. It is

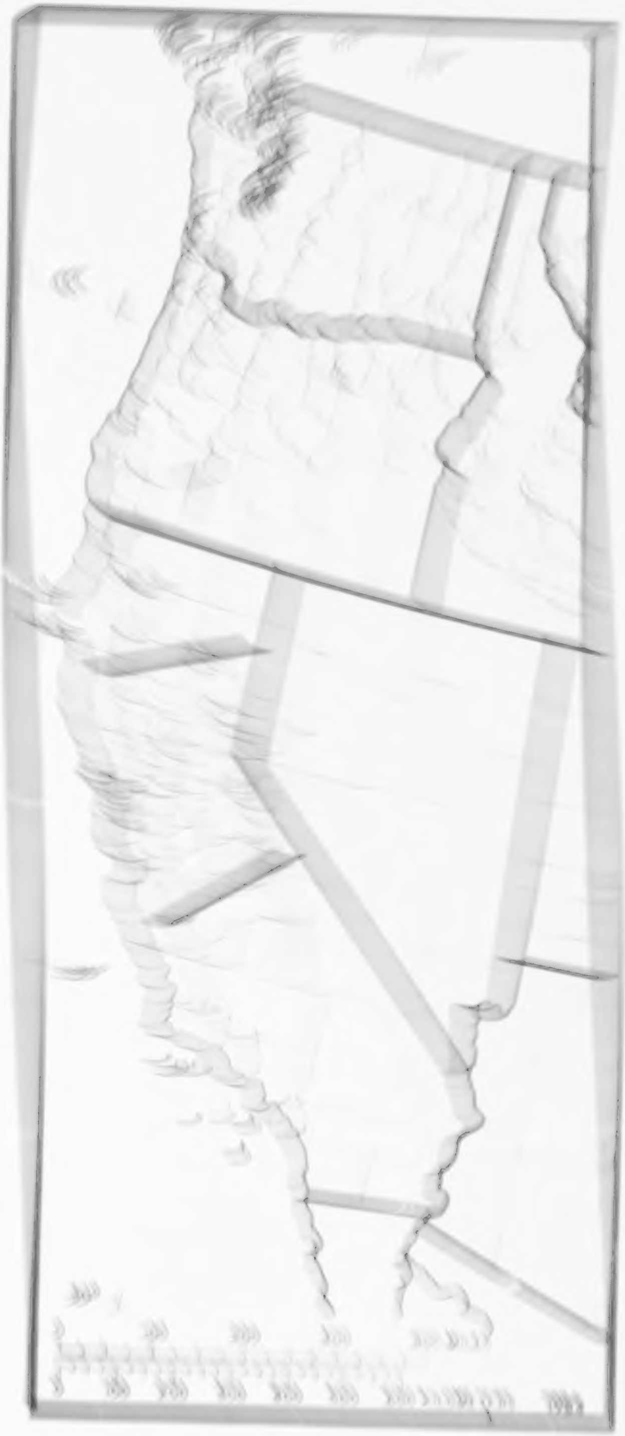

Figure 1—The native range of California red fir.

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d for high-elevation forests, with sum-
ures only occasionally exceeding 29° C
nter temperatures rarely below −29° C
notable climatic feature is a 4- to 5-
r dry spell. Between April (or May) and
cipitation from scattered thunder-
gligible. Almost all precipitation occurs
er and March, with 80 percent or more
wpack can exceed 4 m (13 ft) in the
a, and snow can accumulate to more
t) in Oregon and northwestern Califor-
tal precipitation ranges from 750 to
to 60 in).

n appears to be in areas that receive
) and 1250 mm (30 and 49 in) of
Growth studies on Swain Mountain
Forest, in the southern Cascades of
licate that California red fir grew best
unusually low precipitation (as low as
normal) *(29)*. Low precipitation there
s early snowmelt and a longer growing

ography

ound at high elevations on mountain
ontinue in active formation. The soils
rows are therefore young and fall into
Entisols, Inceptisols, Alfisols, and
ey are classified as mesic to frigid or
an annual soil temperatures (at 50 cm;
n 0° and 15° C (32° and 59° F). All soils
s tend to be light colored, shallow, with
horizon development, and low in cat-
capacity and base saturation. Most are
ome degree as xeric because of the long
eriod. Horizon development is relative-
n the mesic Alfisols. The Spodosols are
rly without a true leached A horizon
dequate warm season precipitation. In
red fir is occasionally found on pumice
ying old soils.

ion of needles and other litter tends to
e wet winter, dry summer climate. Or-
l collects on the surface where it forms
mats from 2 to 8 cm (0.75 to 3.0 in) or
).

h and stand development are best on
ils associated with glacial deposits or
ke beds. On steep slopes where soils
t, stands are open and tree growth poor.
to gentle slopes and flat ground where
ot collect, stands are closed with no
herbaceous vegetation *(8)* (fig. 2).

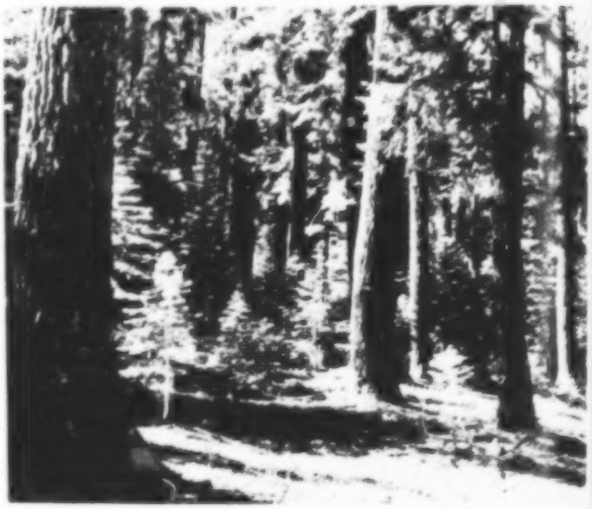

Figure 2—*Old-growth California red fir and California white fir forest at 1950 m (6,400 ft) in the southern Cascades. A lack of understory (right foreground) is common in mature stands on high quality sites. Trees regenerate naturally in small patches (left foreground) as the stand begins to disintegrate.*

Associated Forest Cover

California red fir is a climax species nearly everywhere it is found. It shares climax status with white fir at the upper limit of the white fir zone, although at any given place California white fir *(Abies concolor* var. *lowiana)* or red fir regeneration may predominate *(9,33)*.

Throughout the Sierra Nevada, lodgepole pine *(Pinus contorta)* occupies wet sites within red fir forests. In the south, dry sites are shared with sugar pine *(P. lambertiana)*, mountain hemlock *(Tsuga mertensiana)*, or incense-cedar *(Libocedrus decurrens)*. Scattered individuals of Jeffrey pine *(Pinus jeffreyi)*, sugar pine, and western white pine *(P. monticola)* are found in northern Sierra Nevada forests and as far south as Yosemite in the southern Sierra Nevada *(32,33)*.

In the Coast Ranges of California, Shasta red fir frequently shares dominance with noble fir *(Abies procera)* and is mixed with mountain hemlock and Brewer spruce *(Picea breweriana)* at elevations generally above 1850 m (6,100 ft). On high elevation serpentine soils, Shasta red fir is occasionally found with the more common foxtail pine *(Pinus balfouriana)*, western white pine, and Jeffrey pine *(33)*.

From the southern Cascades north into Oregon and west into the California Coast Ranges, Shasta red fir begins to lose its clear climax status, perhaps as a result of taking on characteristics of noble fir, which is never a climax species in the northern Cascades *(9)*. Shasta red fir is replaced successionally by white fir at the lower elevations and by mountain hemlock at the upper. Major associated species include Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)*, white fir, western white pine, lodgepole pine, and mountain hemlock *(9,33)*.

Red fir is found in seven forest cover types of western North America. It is in pure stands or as a major component in Red Fir (Society of American Foresters Type 207) *(7)*, and also in the following types: Mountain Hemlock (Type 205), White Fir (Type 211), Lodgepole Pine (Type 218), Pacific Douglas-Fir (Type 229), Sierra Nevada Mixed Conifer (Type 243), and California Mixed Subalpine (Type 256).

Brush and lesser vegetation are varied. Dense red fir stands on good quality sites usually have no understory vegetation. In openings resulting from tree mortality or logging, and under open stands on poor sites, many species are possible depending on location *(9,20,42)*. Currant or gooseberry *(Ribes* spp.), pinemat manzanita *(Arctostaphylos nevadensis)*, and mountain whitethorn *(Ceanothus cordulatus)* are the most commonly found brush species *(9,20,21)*. Large brush fields can dominate areas after severe fire. Fir eventually will reclaim these sites as the climax species. With some combinations of low site quality, brush species, and resident rodent population, however, reforestation can be effectively delayed for decades. Small upland meadows are common in red fir forests and provide habitats for a wide variety of sedges, grasses, and forbs.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red fir is monoecious. Male strobili (cones) are small—generally less than 1.6 cm (0.6 in) long—deep purple-red, and densely clustered on the underside of 1-year-old twigs about midcrown. Female cones are borne erect on 1-year-old branches in the uppermost crown, although both male and female cones are occasionally found on the same branch. California red fir flowers from May to June, with pollen shed and fertilization in late May through June. Shasta red fir flowers from middle to late June in southwestern Oregon. Populations in the Coast Ranges of northwestern California probably follow the same schedule. Seeds begin to reach maturity in mid-August and the ripening process continues up to time of seedfall.

Cones are large, 15 to 23 cm (6 to 9 in) long, 5 to 8 cm (2 to 3 in) in diameter, and oblong cylindric in shape. Shasta red fir bracts are longer than the cone scales and are easily visible on the surface of a mature cone. California red fir bracts are shorter than the cone scales and are not visible on an intact cone. Cones of both varieties are brown when mature and have specific gravities of about 0.75 *(8,27,28,36)*.

Seed Production and Dissemination—California red fir can begin producing seed when only 35 to 45 years old; Shasta red fir produces seed when about 5 years younger *(36)*. Heavy seed crops—adequate for reliable regeneration—are produced every 1 to 4 years by California red fir *(22)* and about every third year by Shasta red fir *(12)*.

Seeds are wind-disseminated after cones disintegrate on the trees in late September to mid-October and are dispersed primarily by the prevailing southwesterly winds *(14)*.

In an exceptional year, seed production for both varieties can exceed 1.4 million per ha (570,000/acre) within a stand and along the edge of an opening *(11,14)*. The more frequent "good to heavy" crops may only reach 10 percent of that value. Seed production varies with tree age, size, and dominance. The best, most reliable producers are mature, healthy dominants. Immature fir can produce heavy seed crops, but production is more erratic than that of mature trees *(18)*. California red fir seeds average 14,110/kg (6,400/lb). Shasta red fir seeds tend to be smaller and average 16,095/kg (7,300/lb) *(36)*.

Because cones are borne almost exclusively in the uppermost crown, any top damage caused by insects, diseases, or mechanical agents (for example, wind and snow) directly reduces cone production. Large old trees are prone to such damage. Trees which have lost their tops, however, can frequently develop new terminals and resume cone bearing.

Studies in California indicate that mature dominants along the edge of a clearcutting produce up to twice as many cones as similar trees in closed stands *(18)*. Regeneration data, also from California, indicate that mature trees left in seed tree or shelterwood cuts increase seed production *(25)*.

The number of Shasta fir seeds falling into a clearing decreases rapidly with distance from the stand edge. At a downwind distance equal to about 2 to 2.5 times tree height, seedfall is nearly 10 percent of the stand edge value *(11)*. Dispersal of the heavier California red fir seeds is generally limited to 1.5 to 2 times tree height *(13)*. Germination rates in standard tests are relatively low for both varieties, generally less than 40 percent *(36)*. Even lower field germination rates (5 percent or less) can produce adequate regeneration.

Seedling Development—Red fir seeds germinate in the spring immediately after snowmelt or in, on, and under the snow *(10,14)*. Germination is epigeal. Seeds that germinate several centimeters above ground in the snowpack rarely survive. Seeds that fall before the first permanent snows of winter, therefore, are more effective in producing seedlings. Initial survival is best on mineral soil, perhaps, as in white fir, because presence of appropriate mycorrhizal-forming fungi is increased in the absence of organic layers *(3)*.

Openings created in mixed red and white fir stands in both northern and southern Sierra Nevada tend to regenerate more readily to red fir. Fifty to 80 percent of the regeneration will be red fir, even when the surrounding stand is dominated by white fir *(25,32)*.

Two long-standing assumptions—that red fir growth is extremely slow for the first 20 to 30 years and that snow damage limits height growth—do not appear valid. Recent evidence indicates that beyond the first 5 years, slow growth is not inherent *(16,24)* and snow damage is significant for relatively few seedlings *(17)*. Extended periods of slow early growth appear to result from environmental conditions, such as prolonged shading and browse damage.

Vegetative Reproduction—Under natural conditions red fir does not reproduce vegetatively either by sprouting or layering. Vegetative propagation from cuttings is possible but the techniques currently available are at an early stage of development.

Sapling and Pole Stages to Maturity

Growth and Yield—Red fir volume production is impressive. Normal yield tables for unmanaged stands indicate that a 160-year-old stand on a high site—18 m (60 ft) at 50 years—can carry 2320 m^3/ha (33,150 ft^3/acre). Average sites—12 m (40 ft) at 50 years—carry 1470 m^3/ha (21,000 ft^3/acre) at the same age. These volumes are possible, at least in part, because of the stand density that red fir can maintain. Basal areas on high sites can be well in excess of 126 m^2/ha (550 ft^2/acre) and on average sites in excess of 96 m^2/ha (420 ft^2/acre). In addition, the normal yield tables indicate that stand mean annual increment continues to increase until age 140 *(37)*. Less ideal stands will support slightly less basal area, and mean annual increment may culminate sooner. The capacity of the species to respond to decreases in stand density is impressive, even at the advanced age of 100 years. In stands of white and red fir thinned to 50 percent of their basal area, the remaining trees increased growth sufficiently that overall stand growth was not significantly reduced *(30)*.

Rooting Habit—Root systems of mature forest trees, including red fir, have not been the subject of much research. What little is known has been gleaned from observations of windthrown trees. Mature red fir rooting habit appears to be fairly adaptable, deep and intensive where soil conditions permit or shallow and widespread where rocks or seasonal water tables limit effective soil depth. There is no strong tendency to maintain a single, deep taproot, although rapid development of a strong taproot is critical for survival of new germinants in the dry summer climate.

On at least some sites, however, saplings and poles have large-diameter, carrotlike taproots extending more than 1 m (3 ft) deep, with very poor lateral root development in the upper 30 cm (12 in). This condition has been found on young pumice soils overlying an old, buried profile. Periodic lack of fall snow cover exposes the soil to subzero temperatures and increased temperature fluctuations. Under these conditions pumice soils are subject to ice crystal formation and severe frost heaving. Fine lateral roots are probably killed by mechanical damage during ice formation and frost heaving or, perhaps, by low temperatures.

Red fir is susceptible to windthrow after partial cutting, especially when marginal codominant and lower crown classes are left as the residual stand *(15)*. Root diseases contribute significantly to lack of windfirmness.

Root grafting between red fir trees is indicated by the occasional presence of living stumps *(8)*.

The effects of mycorrhizal associations are beginning to be explored. Early information indicates that these root-fungi relationships are significant in establishment and early growth, especially on poor sites *(3)*.

Reaction to Competition—Although red fir grows best in full sunlight, it can survive and grow for long periods in relatively dense shade. Red fir's tolerance of shade appears to be less than that of mountain hemlock, slightly less than that of white fir and Brewer spruce, but greater than that of all of its other associates. Red fir's capacity to maintain significantly more foliage under shade than white fir suggests that the tolerance difference between them is marginal *(1)*. It is most accurately classed as tolerant of shade. Red fir seedlings are slightly more hardy in full sun than white fir seedlings but become established most easily in partial shade *(14,26)*.

Red fir can carry large basal areas per unit area and maintain high growth rates for an unusually long time, partly as a result of its shade tolerance. As an understory tree it can survive more than 40 years of suppression and, unless diseased, respond to release by increasing growth dramatically. Time until growth accelerates depends on crown condition. Even mature dominants can respond to large reductions in stand density. Seed production on mature dominants can increase after release *(16,25,26,38)*.

Natural regeneration of red fir can be achieved using shelterwood and seed tree cuttings. Clearcuts work as long as the size of the opening perpendicular to the wind does not exceed seed dispersal distances. Site preparation is important *(19)*. Recent developments in nursery and handling technologies, including manipulation of root regeneration capacity and identification of necessary storage and transportation conditions, make artificial planting commercially practical. Access to planting sites is commonly difficult in the Sierra Nevada because of heavy snowpacks that last until June and later.

It is theoretically possible to manage several age classes in a stand because of the species' shade tolerance. However, the ability of red fir to support high growth rates for extended periods in dense, even-aged stands makes even-aged management the likely choice on most sites. Patch cuttings of small areas—0.2 to 2.2 ha (0.5 to 5.5 acres)—work well where larger regeneration cuts are undesirable for visual or environmental reasons.

Damaging Agents—Red fir is subject to damage from abiotic agents, pathogens, insects, and animals. Little is known about the tolerance of red fir to most abiotic aspects of the environment. Initial survival of seedlings seems to be better under partial shade although growth is best in full sunlight. The early advantage of shade may be related to protection from temperatures in exposed duff and litter that can frequently exceed 70° C (160° F) early in the growing season *(14)*.

Red fir appears to be more sensitive to drought than white fir or the associated pines *(26)*, even though over most of its range there may be no precipitation for as long as 5 months during the summer. A tendency of red fir to grow poorly where snowmelt water collects, as on mountain meadows, indicates a moderate sensitivity to high soil moisture content during the growing season *(8)*.

Frosts can occur any month of the year, but damage to red fir is minimal and significant only on Christmas trees. Red fir is more frost resistant than white fir and about equal to Jeffrey pine *(19)*.

The importance of mechanical injury increases as intensive management of dense young red fir stands increases. Studies in Oregon and California show that conventional logging techniques used for thinning or partial cutting damaged 22 to 50 percent of the residual stand. Seventy-five percent of these wounds were at ground level where infection by a decay-causing fungus is almost certain *(2)*. Volume losses by final harvest can be considerable, although the amount varies greatly from place to place, perhaps due to type and frequency of wounds *(2)*.

Among pathogens, one parasitic plant causes major damage. Red fir dwarf mistletoe *(Arceuthobium abietinum* f. sp. *magnificae)* is common throughout the range of red fir and infests 40 percent of the stands in California *(34)*. Heavily infected trees suffer significant growth losses and are subject to attack by *Cytospora abietis*, a fungus that kills branches infected by dwarf mistletoe and further reduces growth. Because of reduced vigor, infected trees are more susceptible to bark beetle attack and other diseases *(34)*. Heart rots, entering through open mistletoe stem cankers, increase volume loss directly and mortality indirectly through stem breakage. Recent unpublished research suggests that losses from bole infection may be of minimal consequence in well-managed second-growth true fir stands *(35)*.

Changes in wood structure in large stem bulges resulting from dwarf mistletoe infections reduce strength of lumber produced. Current lumber grading practices, however, are not adequate to identify the affected wood *(40)*.

Dwarf mistletoe need not be a problem in young managed stands because four factors make damage subject to silvicultural control. Red fir can be infected only by red fir dwarf mistletoe which, in turn, can parasitize only one other fir, noble fir. Small trees (less than 1 m [3.3 ft] tall) are essentially free from infection even in infested stands. Infected young firs, free from new overstory infection, outgrow the spread of mistletoe if height growth is at least 0.3 m (1 ft) per year, and losses from bole infections are expected to be minimal in managed, young-growth stands *(34,35)*. Silvicultural practices that can significantly reduce the impact of dwarf mistletoe include removal of an infected overstory before natural regeneration exceeds 1 m (3.3 ft) in height, and stocking control to promote rapid height growth. Different species can be favored in the overstory and understory of mixed stands during thinnings or partial cutting. Sanitation of stand edges adjacent to regeneration areas and planting a nonhost species

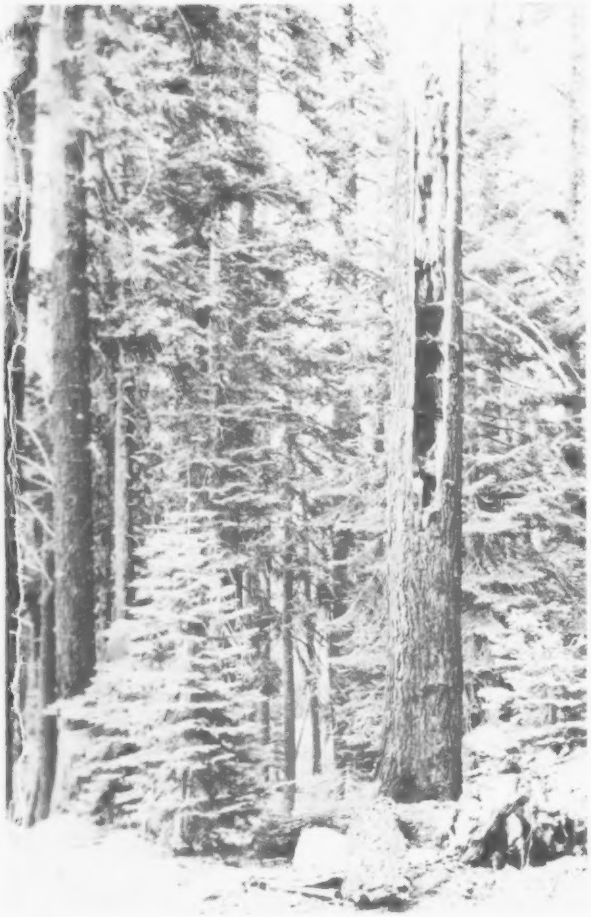

Figure 3—*Mature red fir broken by wind as a result of extensive heart rot.*

(such as white fir adjacent to a red fir stand) appropriate to the site can prevent infection from overstory trees.

Fir broom rust *(Melampsorella caryophyllacearum)* is abundant in the central and southern Sierra Nevada. This disease primarily affects branches but can infect trunks. It can cause spike tops and loss of crown and provide an entry court for heart rots. Fir broom rust can occasionally kill trees, especially seedlings and saplings *(4)*.

Annosus root rot *(Heterobasidion annosum)* is present in all conifer stands and may become a major disease problem as red fir is increasingly and intensively managed. Infection is spread from tree to tree by root contact, forming disease pockets in the stand that slowly expand. Infection of freshly cut stumps or new wounds by aerially spread spores creates new infection centers that do not become evident until 10 to 20 years after infection. Annosus root rot does not usually kill red fir directly, but root damage results in considerable moisture stress and loss of vigor. The loss of vigor predisposes the tree to attack by bark beetles, notably *Scolytus* spp. Direct damage resulting from infection is restricted primarily to heart rot of butt and major roots, leading to windthrow and stem breakage *(4)* (fig. 3). Some degree of control is available through use of borax to prevent infection by *Heterobasidion annosum* in freshly cut stumps.

Other heart rots of major significance include the yellow cap fungus *(Pholiota limonella)* and Indian paint fungus *(Echinodontium tinctorium)*. These fungi cause major losses in old-growth trees. Young trees are generally not affected because they have so little heartwood. Yellow cap fungus tends to be a more severe disease in California, and Indian paint fungus is more severe in Oregon. Yellow cap fungus generally enters through basal wounds. Rot can extend 15 to 18 m (50 to 60 ft) up the trunk. Indian paint fungus probably infects red fir in the same manner as it does western hemlock *(2)*. The fungus enters through branchlets less than 2 mm (0.08 in) in diameter and can remain dormant for as long as 50 years before being activated by injury or stress *(6)*. Dead or broken tops are other points of entry for Indian paint fungus. The resulting rot is located in the upper bole and may extend to the ground. Open dwarf mistletoe cankers serve as entry courts for several decay fungi. None of the heart rots kill directly but predispose the tree to stem breakage. No effective control is known for decay fungi, except possibly *Heterobasidion annosum*, other than avoiding as much root, stem, and top damage as possible during stand management *(4)*.

Insects from five genera attack red fir cones and seeds. Losses can be significant. Cone maggots *(Earomyia* spp.) cause the most damage. Several chalcids *(Megastigmus* spp.) and cone moths *(Barbara* spp. and *Eucosma* spp.) can occasionally cause heavy local damage to seed crops, especially in poor seed years *(13)*.

Cutworms *(Noctuidae)* can be a problem in nurseries and may be especially damaging in natural regeneration areas. Cutworms were responsible for more than 30 percent of the seedling mortality in a study on Swain Mountain Experimental Forest in California *(14)*.

The white fir needleminer *(Epinotia meritana)* is the only foliage feeder of consequence on established red fir. Even during outbreak phases the damage caused is apparently minor and temporary *(13)*.

The most severely damaging insect pest on red fir is the fir engraver *(Scolytus ventralis)*. This bark beetle is found throughout the range of red fir and causes severe damage nearly everywhere. Losses under epidemic conditions can be dramatic. Anything that reduces tree vigor—*Annosus* root disease, dwarf mistletoe, *Cytospora* canker, overstocking, drought, or fire damage—increases susceptibility to fir engraver attack. Several other species of bark beetles *(Scolytus* spp., *Pseudohylesinus* spp.), the roundheaded fir borer *(Tetropium abietis)*, and the flatheaded fir borer *(Melanophila drummondi)* frequently join in attacking and killing individual trees. In epidemic conditions, however, mortality is caused primarily by the fir engraver. Maintenance of stand health and vigor is the only known control *(13)*.

Locally, small rodents can cause significant loss of seed and occasionally girdle seedlings. Squirrels cut and cache cones. Pocket gophers limit regeneration in many areas, particularly clearcuts, by feeding on fir seedlings during winter and spring. Pocket gophers in combination with meadow voles and heavy brush can prevent conifer establishment for decades. Where gopher populations are high, damage to root systems of mature trees can be extensive, although not often identified. In extreme conditions, winter and spring feeding at root crowns can kill trees up to at least 94 cm (37 in) in diameter at breast height *(23)*. Direct control is difficult and expensive. Indirect control by habitat manipulation offers some possibilities.

Spring browsing of succulent growth by deer can retard height growth for many years. Normally, trees are not killed and in most instances can grow rapidly once browsing pressure is removed. In managed stands, reduced height growth can result in significant production loss. Red fir may be damaged less by deer or rabbit feeding than white fir.

Special Uses

Red fir is a general, all-purpose construction-grade wood used extensively as solid framing material and plywood. Good quality young red fir, known as "silvertip fir" from the waxy sheen on their dense, dark-green needles, bring top prices as Christmas trees. These trees are cultured in natural stands and plantations where early growth is slower than most species used as Christmas trees, and some individuals are cultured for as long as 11 years before harvest.

Detailed and exact wildlife censuses for large areas do not exist and any listing of species numbers associated with a major forest type is an approximation. There are, however, about 111 species of birds found in the red fir type of California, 55 of which are associated primarily with mature forests. Perhaps because of the dense nature of most true fir forests, there are only about 52 species of mammals commonly present and only 6 of those are generally associated with mature forests. Few reptilian species are found at the high elevations and only four are generally present in the red fir type.

Genetics

In the northern part of its range, California red fir appears to merge and hybridize with noble fir, a northern species with morphological and ecological similarities. Bracts that extend beyond the scales on mature cones are characteristic of noble fir. North of Mount Lassen, red fir has similar exserted bracts. South of Mount Lassen, bracts on red fir are shorter than the scales and are not visible on intact mature cones. Changes in seed weight, cotyledon number, and cortical monoterpenes in both species indicate a broad transition zone between latitudes 40° and 44° N. Similarity with noble fir increases to the north and west *(41)*. The two species can be artificially cross-pollinated with no apparent difficulty as long as red fir is the female parent. Success is reduced by more than 70 percent when red fir is the male parent *(5,36)*. Discussion continues about the relationship of California red fir, Shasta red fir, and noble fir; however, the fact that exserted bracts also appear on a large southern Sierra Nevada population of red fir that has characteristics in common with both California red fir and Shasta red fir only adds to the controversy *(41)*.

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Abies procera Rehd. **Noble Fir**

Pinaceae Pine family

Jerry F. Franklin

Noble fir (*Abies procera*), also known as red fir and white fir, is an impressive true fir limited to the Cascade Range and Coast Ranges of the Pacific Northwest. At maturity, it typically has a clean, columnar bole and short, rounded crown. Noble fir attains the largest dimensions of any of the true fir species.

Habitat

Native Range

Noble fir (fig. 1) is found in the mountains of northern Oregon and Washington between the McKenzie River and Stevens Pass or latitudes 44° and 48° N. Most of its distribution is within the Cascade Range, particularly on the western slopes and along the crest. Isolated populations are found on peaks in the Oregon Coast Ranges and in the Willapa Hills of southwestern Washington.

Trees with needle and cone characteristics of noble fir have frequently been reported in mixture with California and Shasta red firs (*Abies magnifica* var. *magnifica* and var. *shastensis*) from northern California north to the central Cascade Range in Oregon. Studies of weight of seeds, number of cotyledons, and chemistry of terpenes strongly suggest that the populations north of the McKenzie River differ from the remainder of the fir complex and lack the apparent latitudinal clines in these characteristics found in the populations to the south. In any case, the ecological behavior of the populations from central Oregon south resembles that of California and Shasta red firs much more closely than that of noble fir.

The northern limits of the range of noble fir have also been a source of confusion. Early reports placed noble fir on Mount Baker, in the Olympic Mountains, and at other locations in the northern Cascades. Subsequent investigators have not found noble fir at these Washington sites.

Climate

Noble fir lies entirely within a moist, maritime climatic region. Since it grows primarily at higher elevations—within the *Abies amabilis* zone (*10*)—high precipitation and relatively cool temperatures are characteristic. Five climatic stations within the range of noble fir provide representative data. Annual temperatures average 4.4° to 7.2° C (39.9° to 45.0° F). The mean temperature in January ranges from -4.4° to -1.1° C (24.1° to 30.0° F) and in July, from 13.3° to 16.1° C (55.9° to 60.9° F). Annual precipitation averages 1960 to 2410 mm (77.2 to 94.9 in). About three-fourths of this precipitation occurs between October and March, and much of it accumulates as snowpacks with maximum depths of 1 to 3 m (3 to 10 ft).

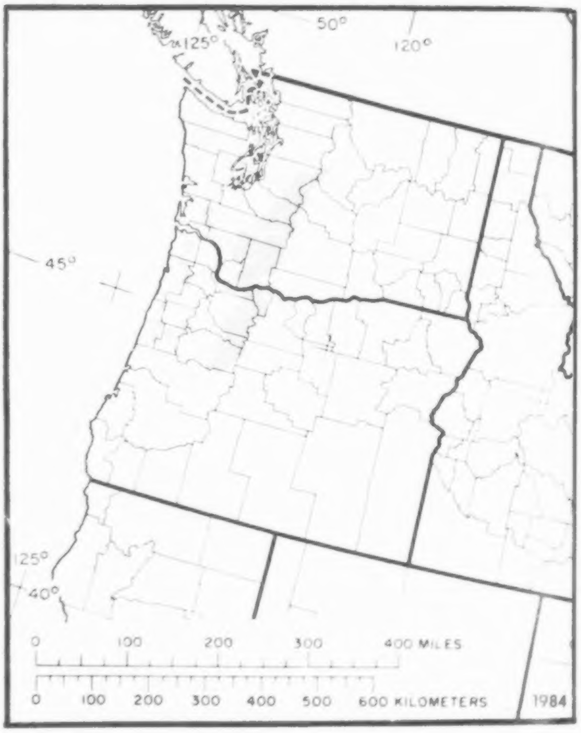

Figure 1—*The native range of noble fir.*

Soils and Topography

Noble fir inhabits rugged, mountainous regions, so steep slopes are typical. It grows on all landforms, from valley bottom to ridgetop. Positions on a slope are perhaps most typical, although the best stands

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are generally on gentle topography. In the northern half of its range, noble fir shows a preference for warm, moist exposures.

Noble fir can grow on a wide range of soils if ample moisture is available; water supply appears to be of more critical importance than soil quality. Spodosols and Inceptisols are most common. In one study of soils under seven upper-slope forest types, soils under noble fir stands had the smallest weight of forest floor (perhaps reflecting favorable decomposition conditions) and the highest levels of exchangeable calcium. Soils are typically developed in volcanic parent materials; volcanic tephra (ash and pumice) and colluvium, often including aerially deposited ejecta, are the most common materials. Profiles with multiple parent materials are often found because of multiple deposits of tephra. In the Coast Ranges, noble fir occurs on both volcanic and sedimentary bedrock.

Noble fir is generally found at elevations between 1070 and 1680 m (3,500 and 5,500 ft) in the Cascade Range in Oregon and 910 and 1520 m (3,000 and 5,000 ft) in the Cascade Range in central Washington. In the Coast Ranges of Oregon, it generally grows above 910 m (3,000 ft). It is occasionally found at much lower elevations, however, and shows excellent growth on such sites.

Associated Forest Cover

Noble fir is associated with most other Pacific Northwest conifers at some point in its range. Most commonly these are Douglas-fir *(Pseudotsuga menziesii)*, Pacific silver fir *(Abies amabilis)*, western and mountain hemlocks *(Tsuga heterophylla* and *T. mertensiana)*, western white and lodgepole pines *(Pinus monticola* and *P. contorta)*, western redcedar *(Thuja plicata)*, and Alaska-cedar *(Chamaecyparis nootkatensis)*. It is also found growing with grand and subalpine firs *(Abies grandis* and *A. lasiocarpa)*, Engelmann and Sitka spruces *(Picea engelmannii* and *P. sitchensis)*, western larch *(Larix occidentalis)*, and whitebark pine *(Pinus albicaulis)*.

Noble fir is a component of five forest cover types *(4)*: Mountain Hemlock (Society of American Foresters Type 205), Western Hemlock (Type 224), Coastal True Fir–Hemlock (Type 226), Pacific Douglas-Fir (Type 229), and Douglas-Fir–Western Hemlock (Type 230). It is a significant component only in Type 226, where noble fir stands are recognized as a major variant.

Most noble fir is found primarily within the *Abies amabilis* zone *(10)* with lesser amounts in the *Tsuga mertensiana* (particularly in Oregon) and *Tsuga heterophylla* (particularly in Washington) zones. It is a component of many recognized plant community and habitat types within these zones *(3,7,9)*. Noble fir presence by habitat type in southern Washington *(9)* is typical of the general pattern. Noble fir is poorly represented on colder sites in the *Tsuga mertensiana* zone and is scarce in the very widespread and environmentally moderate *Abies amabilis/Vaccinium alaskaense* habitat type. It is abundant in the relatively warm, well-watered *Abies amabilis/Tiarella unifoliata* habitat type and in the *Abies amabilis/Xerophyllum tenax* habitat type. Noble fir attains best development on sites characterized by rich herbaceous understories.

Understory plants associated with noble fir typically include an array of ericaceous shrubs and evergreen herbs. Shrubs *(10)* include rustyleaf menziesia *(Menziesia ferruginea)*, Alaska huckleberry *(Vaccinium alaskaense)*, big huckleberry *(V. membranaceum)*, red huckleberry *(V. parvifolium)*, ovalleaf huckleberry *(V. ovalifolium)*, Cascades azalea *(Rhododendron albiflorum)*, Pacific rhododendron *(R. macrophyllum)*, and various currants *(Ribes* spp.). Common herbs include beargrass *(Xerophyllum tenax)*, two trailing blackberries *(Rubus lasiococcus* and *R. pedatus)*, avalanche fawnlily *(Erythronium montanum)*, queenscup *(Clintonia uniflora)*, purple twistedstalk *(Streptopus roseus)*, slim Solomon's seal *(Smilacina sessilifolia)*, coolwort foamflower *(Tiarella unifoliata)*, and white inside-out-flower *(Vancouveria hexandra)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Like other true firs, noble fir is monoecious and produces female strobili high in the crown and clusters of male strobili in a zone below. Female strobili are borne singly or in groups of two, or rarely, up to five, on the upper side of 1-year-old twigs. Male strobili are borne in clusters of up to 30 or more on the undersides of branchlets.

Phenological data for noble fir at three locales and over 3 years show the following ranges in timespans *(12)*:

Male bud burst	May 7 to June 2
Female bud burst	May 11 to June 4
Vegetative bud burst	May 21 to July 5
Pollen shedding	June 1 to July 5
Period of female receptivity	May 25 to July 6
Initiation of seed dispersal	Sept. 27 to Oct. 7

Slightly earlier dates have been recorded for some events *(6)*. Timing of phenological events has varied as much as 2 weeks in 3 years at the same site *(12)*. Events are typically delayed by 1 or 2 days for each 30-m (100-ft) rise in elevation.

Seven developmental stages have been identified for female strobili *(12)*, beginning with bud swelling and ending with cone shattering. A period of early rapid growth coincides with pollen receptivity; this growth period does not appear to be as sensitive to temperature as earlier growth periods. Cone growth is generally completed by mid-August of the same year.

Development of male strobili appears to be sensitive to temperature and humidity; pollen shedding requires warm, dry weather.

Seed Production and Dissemination—Trees may begin bearing cones at 20 years of age, although commercial seed bearing is generally considered to begin at about 50 years. Older trees can produce large quantities of seeds. The current record is an estimated 3,000 cones, potentially yielding more than 1,500,000 seeds, produced by one tree in a single year. In studies extending over the Pacific Northwest Region, noble fir produced a medium or better crop (median cone count of at least 10 cones per tree) 42 percent of the time *(7,13)*. Cone production at particular locations was much poorer, however, especially in the high Cascades and along the eastern margin of the range of noble fir. Individual stands had intervals of as long as 6 years between medium cone crops.

Seed quality is typically poor. Collections from seed traps in natural stands (equivalent to 54 seed years) had a maximum of 49 percent sound seeds; the overall average was about 10 percent. Seed quality is strongly correlated with the cone crop, which must be at least medium size before sound seeds exceed 10 percent *(7)*. Most unsound seeds collected in seed traps consist of round but unfilled seeds, relatively small amounts being damaged by insects.

Possible explanations for the poor seed quality include inadequate pollen (especially in young stands and poor seed years), poor synchrony between female receptivity and pollen shedding *(12)*, selfing, insects, and meiotic irregularities in developing pollen. The most important factors may be similar to those suggested for Pacific silver fir *(24)*. Firs have unspecialized pollen mechanisms, long periods of pollen dormancy, a short time after germination when pollen tubes must develop and penetrate the long nucellar tip, and archegonia that abort quickly if unfertilized. These traits, plus a low number of archegonia, may cause the low percentage of viable seeds.

Noble fir seeds are not widely dispersed because of their weight, which averages 29,750 seeds per kilogram (13,500/lb) *(25)*. Win
dispersal. Although the seed
(2,000 ft) *(22)*, most actually
tree heights of the seed trees
thought that the local distribu
fir was mainly controlled by
capabilities coupled with low r
noble firs in his study area we
narrow in one dimension. In o
wider than the others, noble
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Seedling Development—
transient viability under na
most germinate in the first gro
persal. They remain viable for
forest floor. Germination is ep
germinate freely, and seedlings
or in moderate shade on any m
soil. Initial development of seed
Total height of 1-year-old seedl
to 2.0 in), of which 1 to 3 cm (
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lings typically require 3 to 5 y
of 0.3 m (1 ft).

Seed dispersed after snow c
germinate in and on the snowb
with essentially no chance for
minants.

Natural regeneration of nobl
variable success. In one early
and abundant that it was
hypothesis of reproduction fro
duff *(21)*. Noble fir was dispropo
at regenerating in some small
tions, but it also failed to reg
burn where it consisted of 25 pe
seed source *(29)*. Competing v
regeneration of noble fir on som

Little information is availabl
noble fir after clearcutting.
regeneration is successful; on ot
despite an available seed source
to be superior to that of Dougla
upper-slope habitat types in th
National Forest in Oregon *(28)*.
old clearcuts had 282 to 1,779 n
hectare (114 to 720/acre), depen
Growth was slow; noble fir reac
51 cm (12 to 20 in) at 7 years. I
development of good natural nob
possible, it is not yet predictabl

Early growth of planted se
depending on site conditions and
growth was slow; noble fir seed

cm (2.5 in) tall at the end of the first growing season in the field, half the height of Douglas-fir seedlings planted at the same time. Damage from browsing was much less on noble fir than on Douglas-fir, however. In a test of containerized noble fir seedlings, survival averaged 77 and 60 percent for containerized and bare-root stock, respectively, after 7 years. Total height after 7 years averaged 56 and 46 cm (22 and 18 in) for containerized and bare-root stock, significantly less than for Douglas-fir. Other plantings of noble fir have shown substantially better early growth than these two examples.

Figure 2—[illegible] Willamette National Forest, OR (elevation about 1220 m [illegible]).

Vegetative Reproduction—Noble fir is not known to reproduce vegetatively.

Sapling and Pole Stages to Maturity

Outstanding growth characteristics of noble fir (fig. 2) include its slow initial growth, sustained height growth pattern, and high form factor.

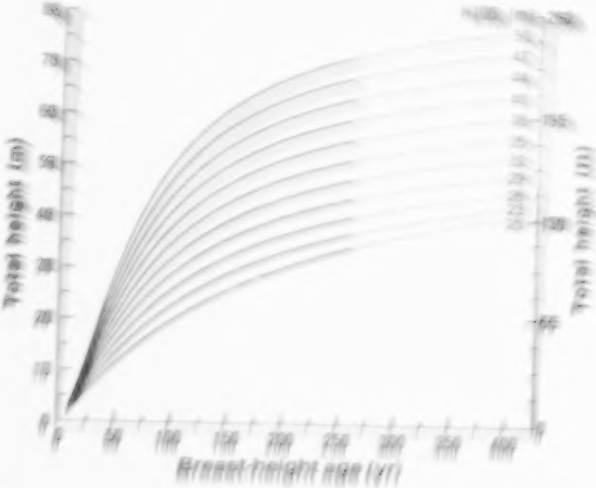

Figure 3—Height growth patterns of natural fire-origin noble fir [illegible] the general range of site qualities (adapted from [illegible]).

Growth and Yield—Initial growth of noble fir is [illegible] show the ability of unmanaged trees to maintain height growth to very advanced ages (200 to 250 years). Maximum heights are greater than 79 m (260 ft) on the best sites, and heights at age 100 (determined at breast height) range from 18 to 49 m (60 to 160 ft).

The largest known noble fir is 274 cm (108 in) in d.b.h., 84.7 m (278 ft) tall, and has a crown spread of 14.3 m (47 ft). Mature specimens are commonly 114 to 152 cm (45 to 60 in) in d.b.h. and 40 to 53 m (132 to 175 ft) tall.

Noble fir grows most frequently in mixed stands with other species, such as Douglas-fir, western hemlock, and Pacific silver fir. It has a greater volume for a given diameter and height than any of its associates and dominates such stands, contributing volume out of proportion to the number of trees. It does grow in nearly pure stands, however, and is capable of producing high standing volumes and good growth over a wide range of ages and site qualities

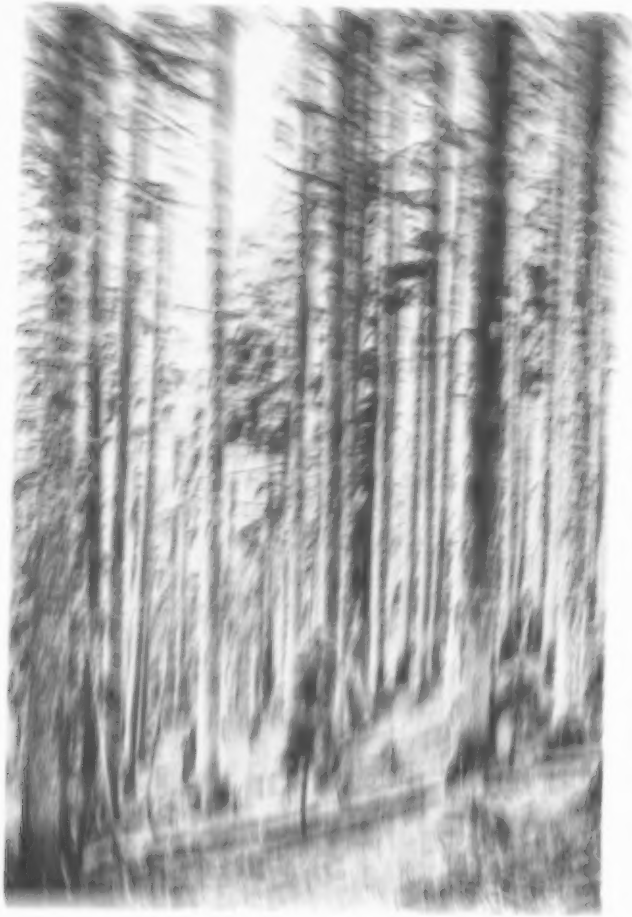

Figure 4.—[illegible]

(7,14) (fig. 4). Sustained height growth, high stand densities, a high form factor, and thin bark all contribute to the development of large volumes of trees and stands. Volumes of about 1400 m³/ha (100,000 fbm/acre) are indicated at culmination of mean annual increment on site class II lands (for example, site index 36 m or 119 ft at 100 years). In the grove at Goat Marsh Research Natural Area on the southwestern slopes of Mount St. Helens in Washington, the gross volume of the best contiguous 1-ha (2.47-acre) block is 5752 m³/ha (82,200 ft³/acre or 407,950 fbm/acre); this value significantly exceeds the best gross volume for an acre of Douglas-fir. British yield tables for noble fir plantations indicate that yields from managed stands should also be high (2).

The high form class (small amount of taper) of noble fir has been noted by many foresters and scientists (23).

Culmination of mean annual increment (MAI) appears to be relatively late in normally stocked stands of noble fir. Volume and, to a lesser extent, MAI increase rapidly in stands from ages 70 to 100 years. The approximate culmination of MAI for site class II (site index of 36 m or 119 ft) seems to be between 115 and 130 years.

Various comparisons of growth have been made between noble fir and Douglas-fir (7,17,23). Site index at 100 years for noble fir is almost always higher than for Douglas-fir on upper-slope habitat types. Despite the slower initial start, noble fir overtops the associated Douglas-firs. Yields of noble fir stands at various ages are 10 to 51 percent higher in board-foot volume and 56 to 114 percent higher in cubic-foot volume than shown in the normal yield tables for Douglas-fir stands of comparable site indexes.

Rooting Habit—The main root of noble fir is [illegible]

[illegible]

Reaction to Competition—Noble fir has the least tolerance for shade of American true firs. Regeneration cannot be established under a closed forest canopy. Consequently, noble fir is considered a seral or pioneer species subject to replacement by its very tolerant associates, Pacific silver fir and western hemlock. It is classed as having intermediate tolerance to shade. Overtopped noble fir saplings and poles may occasionally persist. Seedlings became established in partial shade in the Oregon Coast Ranges (8) and should, therefore, be able to establish themselves successfully under all but the densest shelterwoods. This ability, along with the heavy seed, indicates that shelterwoods or small clearcuts should be the preferred cutting method for natural regeneration of noble fir.

Noble fir prunes itself well in closed stands and develops a short, rounded crown. This short crown, along with an apparent inability to form epicormic or adventitious sprouts, may be a factor in the decline and death of mature noble firs exposed to major stresses, such as along a clearcut boundary. The crown may be unable to sustain the tree when altered temperature or moisture conditions cause higher physiological demands.

Damaging Agents—Insects can be common in cones and seeds. In a study of two locales in a modest seed year, 36 percent of noble fir seeds were affected by insects (26). The fir seed chalcid (*Megastigmus pinus*) was found in 21 percent of the seeds; not all these seeds would necessarily have been filled, however, as the chalcid can develop in unfertilized seeds. Fir cone maggots (*Earomyia barbara* and *E. longistylata*) affected 12 percent and a cone moth (*Eucosma siskiyouana*) 6 percent of the seeds. Other cone insects have been identified by Scurlock (26). One of these, *Dioryctria abietivorella*, can mine buds, shoots, and trunks, as well as cones.

Insects reported as attacking noble fir include two bark beetles (*Pseudohylesinus nobilis* and *P. dispar*) [illegible], a weevil, *Pissodes dubius*, sometimes in association with the fir root bark beetle, *Pseudo-* [illegible]

[illegible] Christmas trees.

Butt and root rots currently known to infect noble fir are *Phaeolus schweinitzii*, [illegible], *Poria subacida*, and possibly *Stereum chailletii*. Hepting (9) identifies no major root diseases that kill noble fir, although such pathogens may exist.

Trunk rots are occasionally important, generally only in overmature timber. The principal trunk rot is Indian paint fungus (*Echinodontium tinctorium*). Others include *Phellinus pini*, *Fomes nobilissimus*, *F. robustus*, *Fomitopsis officinalis*, *F. pinicola*, and *Polyporus abietinus*.

Noble fir in the extreme southern part of its range is attacked by dwarf mistletoe, but this is apparently *Arceuthobium tsugense* and not *A. abietinum* (5). Mistletoe infections have been associated with extensive mortality of branches (5).

Bark is occasionally stripped from the lower boles of pole-size noble firs by black bear. In one 70-year-old stand, more than half the noble firs had large basal scars from such attacks.

Climatic damage to noble fir includes occasional snow breakage of tops and leaders, especially in sapling and pole-size stands; and windbreak and windthrow of mature boles. The species is very tolerant of exposed sites, such as are found along the Columbia River Gorge between Oregon and Washington.

Special Uses

The wood of noble fir has always been valued over that of other true firs because of its greater strength. Loggers called it larch to avoid the prejudice against the wood of true fir; the two Larch Mountains opposite one another across the Columbia River near Portland, OR, were named for the noble fir that grows on their summits. Because of its high strength-to-weight ratio, it has been used for specialty products, such as stock for ladder rails and construction of airplanes.

In [illegible], noble fir constituted about 12 percent of the Christmas tree production in the Pacific Northwest [illegible]

[illegible] for ornamental planting and landscaping.

Genetics

[illegible] mination of seeds or in survival after 3 years. The number of cotyledons was greater for selfed individuals, but 5- and 10-year height growth was less. Survival of outplanted outcross trees did not differ after 10 years from that of wind-pollinated and selfed trees.

Population Differences

Variation in cotyledon number and seed weight (11), monoterpenes (32), and seedling characteristics has been studied in noble fir populations. Substantial variability exists in cotyledon number and seedling characteristics but does not appear to be related to latitude. Furthermore, noble fir appears discontinuous in characteristics from the fir populations south of the McKenzie River in Oregon. The southwestern Oregon populations may be a part of a strong latitudinal gradient that includes California red fir and extends south to the Sierra Nevada and California Coast Ranges.

Races and Hybrids

No races of noble fir are known within its natural range, but three horticultural varieties *(glauca, prostrata,* and *robustifolia)* are known.

Noble fir has been artificially crossed with several other true firs. It interbreeds readily with California red fir, and reciprocal crossings have high yields of viable seed. Some noble fir parents yield nearly as much seed from pollen of California red fir as from local noble fir pollen. Other crossings reported in the literature are *Abies concolor* (supposedly "confirmed"), *recurvata, sachalinensis, balsamea,* and *lasiocarpa.* None of these have been repeated, however, and all are seriously questioned as to validity.

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Chamaecyparis lawsoniana (A. Murr.) Parl. **Port-Orford-Cedar**

Cupressaceae   Cypress family

Donald B. Zobel

Port-Orford-cedar *(Chamaecyparis lawsoniana)*, also called Lawson cypress and Port Orford white-cedar, is known for its grace in ornamental plantings and for its versatile wood. As logs, mostly exported to Japan, it brings higher prices than almost any other conifer in the United States. This valuable tree, however, has a very limited range and an uncertain future. Management of Port-Orford-cedar has become impossible in much of its range since the introduction of a fatal root rot that is still spreading. Old-growth forests are being depleted rapidly, and the use of second-growth forests is complicated because early growth is relatively slow. The commercial future of one of the most beautiful and potentially useful trees will depend on development of silvicultural practices that minimize infection by root rot.

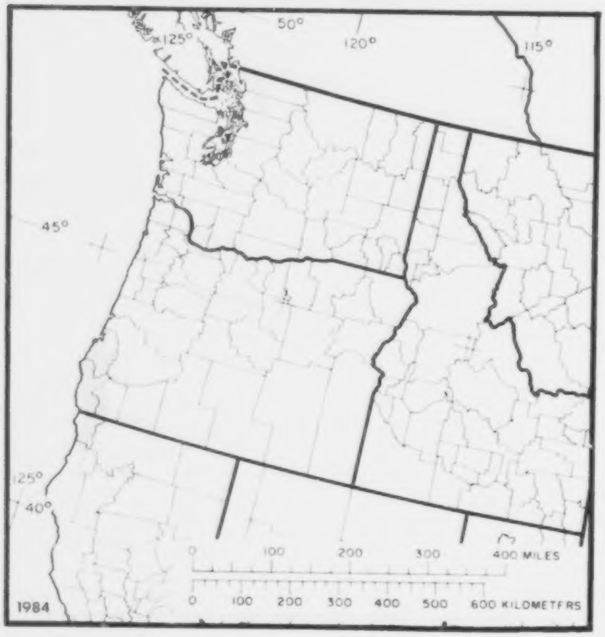

Figure 1—*The native range of Port-Orford- cedar.*

Habitat

Native Range

Port-Orford-cedar (fig. 1) grows in a small area near the Pacific coast, from about latitude 40° 50′ to 43° 35′ N. in southern Oregon and northern California *(13)*. It is most important on uplifted marine terraces and in the Coast Ranges of southern Coos County and northern Curry County, OR. A secondary concentration is found at high elevations in the upper reaches of the Illinois and Klamath River drainages near the Oregon State boundary. Throughout the rest of its range, Port-Orford-cedar is found as small, scattered populations, most common in the drainages of the middle Rogue, upper Illinois, Smith, lower Klamath, and lower Trinity Rivers. A major inland disjunction includes small populations of the upper Trinity and Sacramento River drainages southwest of Mount Shasta, CA.

Climate

The Pacific Ocean strongly influences the climate of most of the range of Port-Orford-cedar. Winters are cool and wet; summers are warm and dry *(13)*. Precipitation is moderate to high, usually 1000 to 2250 mm (39 to 89 in); only 2 to 4 percent occurs from June to August. A snowpack of 1 to 2 m (3 to 7 ft) is common at the higher elevations of the Klamath Mountains. Humidity remains high at night in most areas, although some interior valley sites have dry air during the day. Fog is common along the immediate coast and during the morning in some smaller interior valleys; summer cloudiness is most common near the northern end of the range. Temperatures varied widely in 2 years of measurement *(13)*. At three coastal sites, monthly average understory air temperatures at 1 m (3 ft) ranged from 5° C (41° F) in January to 14° C (57° F) in July; the mean annual temperature was 8.5° C (47° F). At the warmest site at 360 m (1,180 ft) near Kerby, OR, monthly averages were 3° to 22° C (37° to 72° F) and annual average was 11.3° C (52° F); at the coldest site, southwest of Mount Shasta, CA, at 1520 m (4,980 ft), monthly averages were –2° to 14° C (29° to 57° F) and annual average was 5.2° C (41° F). The lowest air temperature measured in a Port-Orford-cedar stand was –15° C (5° F) at a height of 1 m (3 ft). Soil temperatures at 20 cm (8 in) below the surface were generally cool; the annual mean was 4° to 11° C (39° to 52° F). The

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average difference between the warmest and coldest month was 8° C (14° F). Apparently the soils seldom freeze; the minimum temperature measured was -0.5° C (31° F).

Coastal winds in summer are primarily from north to northwest; they strike the coast at an angle at the north end of the range, driving moist air ashore and up the Coquille River Valley. This may influence the superb development of Port-Orford-cedar in this part of its range.

Soils and Topography

Port-Orford-cedar grows on many geologic and soil types: sand dunes; bogs, margins of intermittent streams, and drier sites on ultramafic rocks; and productive soils on sedimentary rocks and diorite *(13)*. The largest trees are found on deep soils weathered from sedimentary rocks in Coos County, OR. The species is also found on sedimentary rocks near the lower Klamath River in California. Throughout much of its range, it is restricted to areas with consistent seepage within a meter of the soil surface. South of Coos County, OR, it is most common on wet spots on ultramafic rocks, especially at lower elevations in the inland and southern parts of its range. Reportedly, Port-Orford-cedar grows on soils in the orders Spodosols, Ultisols, and Inceptisols.

Soils vary from well developed, deep, and productive to skeletal (in seepage areas on peridotite) *(13)*. Average depth to the surface of the C horizon ranges from 32 cm (13 in) in the mixed pine community to 73 cm (29 in) in the rhododendron community. Surface soils vary from sandy loam to clay in texture and often contain much gravel, cobble, or stone; their pH values range from 4.2 to 7.0; cation exchange capacities range from 10 to 42 meq/100 g. Concentrations of macronutrients are nitrogen, 0.12 to 0.25 percent; phosphorus, 2 to 40 p/m; extractable potassium, 36 to 400 p/m; extractable calcium, 0.3 to 10.8 meq/100 g; extractable magnesium, 0.2 to 9.9 meq/100 g. Calcium-to-magnesium ratios are 0.2 to 3.7. Foliar concentrations of nutrients in native saplings are often low (means for 85 saplings at 10 sites were 0.86 percent nitrogen, 0.52 percent potassium, and 0.11 percent phosphorus); in contrast, calcium is usually quite high (1.11 percent) *(13)*. The calcium-to-magnesium ratio of foliage is high, averaging 4.4 and staying above 2 even on ultramafic substrates. Surface soils under Port-Orford-cedar plantations in Great Britain have the highest pH of soils under any conifer tested. Growth in the northern end of the natural range increases with levels of nitrate in the soil. In culture, growth increases with levels of potassium, nitrogen, and calcium in the foliage *(13)*.

In some areas in the northern part of its range, Port-Orford-cedar grows in habitats similar to those of western redcedar *(8,9)*. On sites where both species are present, soils under Port-Orford-cedar are usually more acidic and have higher concentrations of potassium and lower calcium:magnesium ratios. Mineralization of nitrogen is slower in Port-Orford-cedar litter.

Port-Orford-cedar usually grows on concave or sheltered slopes where soil seepage occurs *(13)*. It is most common on slopes, on benches, and in drainageways. Restriction to streamsides and ravines is most obvious inland at low elevations. Stands are most common on northwest, north, and northeast aspects, especially at lower elevations. Port-Orford-cedar grows from just above sea level to about 1500 m (4,900 ft) in the main section of the range, and to 1950 m (6,400 ft) near Mount Shasta *(13)*.

Associated Forest Cover

Port-Orford-cedar is found with an extremely wide variety of associated plants and vegetation types. It usually grows in mixed stands and is important in the *Picea sitchensis*, *Tsuga heterophylla*, mixed evergreen, and *Abies concolor* vegetation zones of Oregon *(3,13)* and their counterparts in California *(1)*. It also grows in a variety of minor communities from dry sand dunes to *Darlingtonia* (cobra-lily) bogs. The species reaches its greatest size and commercial worth in the dense, rapidly growing forests of the *Picea sitchensis* and the *Tsuga heterophylla* zones (fig. 2), in which Douglas-fir often dominates. Port-Orford-cedar is most dominant on wet soils, most of which have parent material at least partially ultramafic, in the high elevation *Abies concolor* zone where forests are dense but slow growing *(13)*. In the mixed evergreen zone, it is the only shade-tolerant conifer in most stands. On drier sites on ultramafics and in bogs, forests can be very open and slow growing. The cedar is dominant in the forest cover type Port-Orford-Cedar (Society of American Foresters Type 231) *(2)* and is listed as a minor associate for parts of the following types: Sitka Spruce (Type 223), Pacific Douglas-Fir (Type 229), Redwood (Type 232), Oregon White Oak (Type 233), and Douglas-Fir–Tanoak–Pacific Madrone (Type 234).

Major communities in old-growth forests where Port-Orford-cedar is a major component include the following, named for the apparent dominants at climax (abbreviated names are given in parentheses) *(13)*:

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Tsuga heterophylla zone

Tsuga heterophylla–Chamaecyparis lawsoniana / Polystichum munitum–Oxalis oregana (swordfern); *Tsuga heterophylla–Chamaecyparis lawsoniana / Rhododendron macrophyllum–Gaultheria shallon* (rhododendron); *Chamaecyparis lawsoniana–Tsuga heterophylla / Xerophyllum tenax* (bear grass).

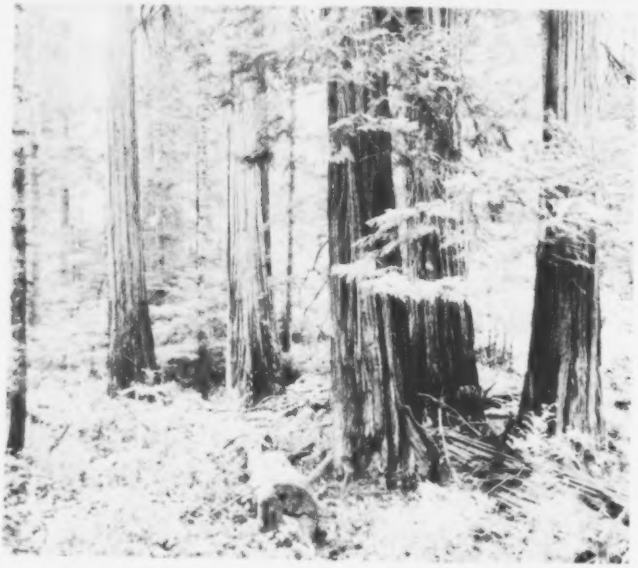

Figure 2—*Old-growth Port-Orford-cedar forest on productive soil developed from sedimentary rocks, on a bench in the Coquille River Falls Research Natural Area, Coos County, OR.*

Mixed evergreen zone

Chamaecyparis lawsoniana / Lithocarpus densiflorus (tanoak); *Pinus–Chamaecyparis lawsonina / Quercus vaccinifolia / Xerophyllum tenax* (mixed pine).

Abies concolor zone

Abies concolor–Tsuga heterophylla–Chamaecyparis lawsoniana (white fir-western hemlock); *Abies concolor–Chamaecyparis lawsoniana* / herb (white fir); *Abies–Chamaecyparis lawsoniana* / herb (mixed fir).

Port-Orford-cedar is less common in a wider variety of forest communities.

Plants of major importance associated with Port-Orford-cedar vary among zones *(6,13)*. Trees are Sitka spruce *(Picea sitchensis)*, western hemlock *(Tsuga heterophylla)*, Douglas-fir *(Pseudotsuga menziesii)*, tanoak *(Lithocarpus densiflorus)*, sugar pine *(Pinus lambertiana)*, Jeffrey pine *(P. jeffreyi)*, western white pine *(P. monticola)*, redwood *(Sequoia sempervirens)*, white fir *(Abies concolor)*, and Shasta fir *(A. magnifica* var. *shastensis)*.

Shrubs are Pacific rhododendron *(Rhododendron macrophyllum)*, western azalea *(R. occidentale)*, evergreen huckleberry *(Vaccinium ovatum)*, red huckleberry *(V. parvifolium)*, salmonberry *(Rubus spectabilis)*, cascara buckthorn *(Rhamnus purshiana)*, California buckthorn *(R. californica)*, salal *(Gaultheria shallon)*, Pacific bayberry *(Myrica californica)*, huckleberry oak *(Quercus vaccinifolia)*, Sadler oak *(Q. sadleriana)*, western leucothoe *(Leucothoe davisiae)*, Pacific yew *(Taxus brevifolia)*, Oregongrape *(Berberis nervosa)*, and Oregon boxwood *(Pachistima myrsinites)*.

Important herbs are swordfern *(Polystichum munitum)*, Oregon oxalis *(Oxalis oregana)*, beargrass *(Xerophyllum tenax)*, western twinflower *(Linnaea borealis* var. *longiflora)*, vanillaleaf *(Achlys triphylla)*, prince's-pine *(Chimaphila umbellata* var. *occidentalis)*, Hooker fairybells *(Disporum hookeri)*, western starflower *(Trientalis latifolia)*, and inside-out-flower *(Vancouveria* spp.).

The general relationships of well-developed Port-Orford-cedar forests to rock type, geographic location, and elevation are shown in figure 3. These forests have 75- to 86-percent cover by trees more than 15 cm (6 in) in d.b.h., except the mixed pine community, which has 39 percent. Tree reproduction is often abundant, and density of trees less than 15 cm (6 in) in d.b.h. ranges from 1246/ha (rhododendron community) to 4113/ha (white fir) (504 to 1,664/acre); 26 percent (swordfern) to 78 percent (tanoak) of these are Port-Orford-cedar; cover of tree reproduction ranges from 30 to 46 percent.

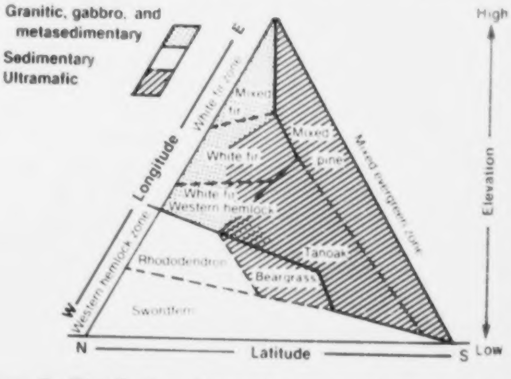

Figure 3—*Distribution of vegetation zones and eight major forest communities of old-growth Port-Orford-cedar, in relation to soil parent material, elevation, and geographic location. Zones are separated by solid lines, communities by broken lines (modified from 6).*

Shrub cover is very dense in rhododendron and tanoak communities (over 90 percent), moderate to dense in most communities (30 to 67 percent), but only 9 percent in the swordfern community. Moss cover is high in the *Tsuga* zone.

Representation of Port-Orford-cedar is usually lower in the forest than in the cedar-dominated communities described above *(13)*. For example, on 3752 ha (9,271 acres) of the former Port Orford Cedar Experimental Forest in southern Coos County, OR, 28 percent of total timber volume was Port-Orford-cedar. Cedar volume exceeded 50 percent on 41 percent of the area, was 25 to 50 percent on 7 percent of the area, 10 to 24 percent on 15 percent of the area, and less than 10 percent on the remainder.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pollen and seed cones develop on the same branches of this monoecious species. Reproductive organs are initiated in late spring or summer. They soon protrude beyond the surrounding leaves, and development continues through the summer. The bladderless pollen is formed in late winter in the bright red pollen cones; on the Oregon coast it is shed about mid-March. Fertilization occurs a month or more later, and seeds mature in September or October of the same season *(5,13)*. Each fertile scale of the 7 to 10 scales in the globose cone usually bears 2 to 4 seeds. Cones contain about 20 percent of their weight in seeds *(5)*.

Seed Production and Dissemination—Seed production starts when the tree is 5 to 20 years old *(5)*. It can be induced in trees as young as 7 months with sprays of 50 p/m gibberellic acid (the effect is enhanced by Ethrel) with the correct photoperiodic regime *(13)*. (At least 2 weeks of long days are required after gibberellin treatment, followed by at least 2 weeks of short days, followed by long days to allow cone maturation.)

The major peak of seedfall is in the late fall, with a smaller one in spring. Roughly 50 to 60 percent of the seeds fall by mid-January and 85 to 90 percent by May 1 *(13)*; however, some seed is released all year.

Crops of 20,000 to 4,600,000 seeds per hectare (8,094 to 1,862,000/acre) have been measured, with a mean of 829,000 seeds per hectare (335,000/acre) for 30 crops *(13)*. Annual seed production can also be expressed in relation to a unit basal area of the population; 600 to 185,000 with a mean of 40,200 seeds per square meter (56 to 17,187 with a mean of 3,735/ft^2) of basal area were produced. Of 30 crops, 5 exceeded 100,000 seeds per square meter (9,290/ft^2) of basal area, 6 produced 20,000 to 60,000 seeds per square meter (1,858 to 5,574/ft^2), 6 had 10,000 to 20,000 seeds per square meter (929 to 1,858/ft^2), and 13, less than 10,000 seeds per square meter (929/ft^2). High seed production per unit basal area occurred in all types of habitats sampled and in both 65-year-old and old-growth forests. No site had good or moderate seed crops 2 years in succession. There seems to be no regional synchronization of large seed crops, however, as occurs in many tree species.

The seeds are small, averaging about 463 000/kg (210,000/lb), with a range of 176 to 1323/g (80,000 to 600,000/lb) *(5)*. Despite having small wings along both sides, the seeds apparently fall more rapidly than many larger conifer seeds. The seed wings appear to aid their flotation on water. Seeds are not a preferred food of rodents in feeding experiments *(7)*, but harvesting of large numbers of cones and removal of seed from them by rodents have been observed in natural stands *(13)*.

Seeds may be stored frozen at less than 10-percent moisture in a sealed container for more than 10 years and retain considerable viability *(5,12)*. One study reports 43-percent germination from seed stored this way for 13 years. Few seeds, if any, germinate later than the first year after dispersal *(13)*.

Seedling Development—Seed germination is epigeal; in the natural habitat, it occurred in early June or later in the 1 year it was observed *(13)*. Germination ranged from 11 to 44 percent in natural seed fall trapped on the floor of seven forests. Germination of collected seed is often higher, about 50 percent *(5)*.

Stratification increases germination and seedling growth for some seed lots *(13)*. Red light accelerates germination; far-red light delays it. In laboratory conditions, few seeds germinate below 12° C *(12)*. Sowing in the nursery in March and April is more reliable in England than fall sowing *(13)*. In nursery practice, seeds were sown at 320 to 540/m^2 (30 to 50/ft^2) and covered by 3 to 6 mm (0.12 to 0.25 in) of soil *(5)*. Shading until midseason may be helpful. A nursery yield of 284,000 usable plants per kilogram of seed (129,000/lb) has been reported *(5)*. Port-Orford-cedar seedlings are easy to grow and establish *(13)*. Seedlings have been planted as 2-0 or 3-0 stock in the United States, and after the first or second year, or as 2-1 stock in Great Britain. Spacing in Britain is 1.4 to 1.5 m (4.5 to 5 ft); recently, in its native range, Port-Orford-cedar has been interplanted with Douglas-fir, at 2.7- to 8-m (9- to 26-ft) spacing *(13)*.

Seedlings are small, with two cotyledons. The next several whorls of leaves are needlelike (5 to 13 whorls in one study); successive whorls gradually develop into the mature, appressed, scalelike foliage differentiated into the flat "facial" and the folded "lateral" leaves *(13)*. Seedling establishment in small experimental plots under a natural canopy was most common where soil had been disturbed but did occur in natural litter; after three growing seasons, only 5 percent of the germinants survived in the most favorable soil conditions. In clearcut or partially cut areas, establishment decreases as ground cover vegetation increases *(7)*.

Seedling growth under a canopy is slow—experimental seedlings are only about 40 mm (1.6 in) tall after their second growing season *(13)*. Seedlings in the open average 36 mm (1.4 in) after 1 year and 78 mm (3.1 in) after 2. Planted 3-0 stock averaged 48 cm (18.8 in) tall after 2 years in the field *(7)* Natural seedlings established under a canopy take 14 to 31 years to reach breast height (1.37 m; 4.5 ft), compared with 5 to 11 years for trees in clearcuts on nonultramafic soils *(13)*. Early seedling growth sometimes equals that of Douglas-fir in the same clearcut. Seedlings are quite shade-tolerant but do die in dense shade under old-growth forest and do not become established under young, dense, even-aged stands *(13)*. They seem to survive in most understory microsites where western hemlock and white fir can grow.

Port-Orford-cedar often reproduces aggressively from seed. Natural reproduction in clearcuts is usually adequate within 80 to 110 m (262 to 361 ft) of a seed source; however, planting will often be required in large clearcuts *(13)*. Planted seedlings may grow normally in dense competition from gorse or bracken fern. Later growth is intrinsically somewhat slower than that of Douglas-fir *(13)*, and weeding may be necessary to keep Port-Orford-cedar in the upper canopy where maximum growth is possible.

Port-Orford-cedar does not develop winter buds with preformed internodes *(13)*. Elongation continues for as long as 5 months in mild coastal climates; it is more rapid and early in the mixed evergreen zone and equally rapid but late in the *Abies concolor* zone. Elongation lasts 1.3 to 1.9 times as long as that of Pinaceae on the same site.

Vegetative Reproduction—Cuttings may be rooted with relative ease *(13)*. A recommended practice is to use cuttings from tips of major branches from the lower crown of young trees, taken from December to February. Auxin treatments sometimes aid rooting. Natural layering of Port-Orford-cedar occurs occasionally *(13)*. Several vertical limbs of windthrown trees in open stands may develop into separate trunks attached to the horizontal "parent" trunk. Most reproduction, however, is from seed.

Sapling and Pole Stages to Maturity

Growth and Yield—After the sapling stage, growth of Port-Orford-cedar is considerably slower than that of Douglas-fir, except on ultramafic substrates where the cedar is usually exceeded in size only by sugar pine *(13)*. In 8- to 26-year-old plantations in the Pacific Northwest, annual height growth of unbrowsed Port-Orford-cedar averaged 0.35 m (1.15 ft), only 86 percent of the mean annual height growth of Douglas-fir; the difference was much greater for browsed trees. In mixed stands, Port-Orford-cedar is usually overtopped by 20 to 25 years. Pole-size stands in the northern part of the range show a large difference in both diameter and height between Douglas-fir and cedar. In one small sample of 53- to 60-year-old trees (age determined at breast height) in coastal Coos County, OR, the Douglas-fir averaged 73 cm (29 in) in d.b.h. and 38 m (125 ft) in height; the cedar averaged 47 cm (19 in) and 28 m (92 ft). Measurements of adjacent stumps on several sites throughout the range showed that the diameter of Port-Orford-cedar was 57 percent that of Douglas-fir at 100 years; however, the difference decreased with age, cedar becoming 74 percent of the diameter of Douglas-fir at 200 years, 78 percent at 300, and 90 percent at 400 *(13)*. Diameter growth of cedar is thus more consistent throughout its life than is that of Douglas-fir.

Size of old-growth cedar trees is variable; much variation is associated with the habitat (and thus the forest community) *(13)*. Early rapid height growth in open stands on ultramafic rocks is not sustained. For example, a sample of forest-grown 90- to 110-year-old trees averaged 30 m (98 ft) in height in the swordfern community, 18 m (59 ft) in the mixed pine community on ultramafics, and 12 to 13 m (39 to 43 ft) in other communities. By 190 to 210 years, heights were 47 m (154 ft) for swordfern, 25 to 29 m (82 to 95 ft) for other communities, but only 21 m (69 ft) for the mixed pine community. At 290 to 310 years, values were 63, 31 to 50, and 29 m, respectively (207, 102 to 164, and 95 ft). Average diameters in old-growth stands range from 42 cm (17 in) (diameter of a tree of mean basal area, mixed pine community) to 86 cm (34 in) (swordfern). Trees more than 100 cm (39 in) in d.b.h. occur in many old-growth stands, and trees of 200 to 250 years may reach 100 cm, but most trees this size are older than 300. On the other hand, one 37-cm (15-in) tree in the mixed pine community

Table 1—Attributes of British plantations of Port-Orford-cedar and western redcedar for the least productive (A) and most productive (B) yield classes[1]

Stand	Trees		Height		Diameter		Basal area maintained after thinning		Cumulative yield	
age	A	B	A	B	A	B	A	B	A	B
yr	*no./ha*		*m*		*cm*		*m²/ha*		*m³/ha*	
20	3,575	2,186	8	13	10	14	28	35	50	232
40	1,730	746	16	24	18	30	42	54	377	901
60	984	451	21	30	26	43	51	66	706	1,439
80	738	347	24	35	32	53	59	76	953	1,838
yr	*no./acre*		*ft*		*in*		*ft²/acre*		*ft³/acre*	
20	1,447	885	26	43	3.9	5.5	122	152	715	3,315
40	700	302	52	79	7.1	11.8	183	235	5,388	12,876
60	398	183	69	98	10.2	16.9	222	287	10,090	20,565
80	299	140	79	115	12.6	20.9	257	331	13,620	26,267

[1] Yield classes A and B support maximum mean annual increments of 12.0 and 24.0 m^3/ha (171.5 and 343.0 ft^3/acre), respectively. Yields include thinnings and are computed for top diameter of 7 cm (2.8 in) outside bark (adapted from *13*)

was more than 300 years old. Maximum tree age exceeds 560 years *(13)*.

Relatively few yield values exist for young stands. Experience in Great Britain is limited but well documented *(13)*; Port-Orford-cedar is combined with western redcedar in yield tables (table 1). Thinnings begin at 20 to 30 years. Mean annual increment (MAI) peaks at 57 to 72 years. Current annual increment (CAI) increases later than for Douglas-fir and western hemlock on good sites and after its peak decreases more slowly than Douglas-fir but faster than hemlock. On poor sites, CAI starts to increase late than for Douglas-fir but earlier than for hemlock; it decreases after Douglas-fir but before hemlock. On good sites, peak MAI is reached 5 years later than for Douglas-fir and hemlock; on poor sites, it is reached 10 years later than for Douglas-fir but 5 years earlier than for hemlock. In one study, cedar plantations at 60 years were maintained at two to three times the density of Douglas-fir with 1.4 to 1.5 times higher basal area. Sixty-year-old trees averaged 5 to 8 m (16 to 25 ft) shorter and 11 to 20 cm (4 to 8 in) smaller in diameter breast height than Douglas-fir.

Volumes reported from young natural stands in Oregon (table 2) and plantations in Europe and New Zealand *(13)* are in the moderate to low range, compared with British plantations; however, the small top diameter limit used for table 1 and the impurity of natural stands may account for most or all of the difference. Values of MAI for two Oregon stands (table 2) were 13.7 (61 years) and 16.9 m^3/ha (57 years) (196 and 242 ft^3/acre).

Live volumes of Port-Orford-cedar in old-growth forest sampled in 1935–40 averaged 86 m^3/ha (1,229 ft^3/acre) in the valley of the South Fork of the Coquille River (Port Orford Cedar Experimental Forest, 3752 ha or 9,271 acres); the most volume in a 259-ha (640-acre) section was 154 m^3/ha (2,201 ft^3/acre) *(13)*. Average volume near Bluff Creek, southwest of Orleans, CA, in 1940 was 22 m^3/ha (314 ft^3/acre) and the maximum was 47 m^3/ha (672 ft^3/acre) on 4922 hectares (12,162 acres). Most volume was in large trees. On coastal terraces, the proportion of Port-Orford-cedar decreased as total volume of old-growth timber increased *(13)*.

Rooting Habit—A dense, coastal 50-year-old stand of Port-Orford cedar on a clay-loam soil had a dense network of fibrous roots at the surface *(4)*. The major horizontal system of surface roots extended up to 7 m (22 ft) from the trunk, producing "humus strivers" (roots with unlignified tips that rise into the surface soil and duff) uniformly along its length. Root systems of adjacent trees intermingled freely; some overlap was likely in trees closer than 12 m (39 ft). Root grafting was common in the main horizontal surface root system, averaging 1.5 grafts per tree; the average graft was 34 cm (13 in) deep between roots 3.8 cm (1.5 in) in diameter. The chance of grafting decreased with both horizontal distance between trees (becoming very small beyond 6 m (20 ft)) and with vertical distance on the slope; however, graft complexes that included several trees sometimes joined trees as far as 12 m (39 ft) apart. Port-Orford-cedar has no taproot but produces vertical sinkers from the horizontal system.

Port-Orford-cedar forms endomycorrhizae with fungi of the family Endogonaceae *(13)*.

Reaction to Competition—Port-Orford-cedar is tolerant of shade and of competition in natural

Table 2—Yields from young natural stands of Port-Orford-cedar in western Oregon *(7)*

Location	Stand age	Total stand all species: Trees	Total stand all species: Basal area	Port-Orford-cedar: Trees	Port-Orford-cedar: Basal area	Port-Orford-cedar: Average diameter	Port-Orford-cedar: Average height[1]	Port-Orford-cedar: Volume
	yr	*no./ha*	*m^2/ha*	*no./ha*	*m^2/ha*	*cm*	*m*	*m^3/ha*
Coos County Forest	36	3,361	68	2,026	41	16	16	244
Coos County Forest	40	2,817	72	1,359	36	18	16	205
Coos-Curry county line	44	1,853	94	1,507	66	24	22	506
Coos-Curry county line	43	1,705	80	1,384	51	22	22	445
Port Orford	61	1,680	113	1,458	90	28	23	838
Port Orford	57	1,666	126	1,483	115	31	22	966
	yr	*no./acre*	*ft^2/acre*	*no./acre*	*ft^2/acre*	*in*	*ft*	*ft^3/acre*
Coos County Forest	36	1,360	298	820	179	6.3	51	3,490
Coos County Forest	40	1,140	312	550	157	7.2	52	2,930
Coos-Curry county line	44	750	408	610	287	9.3	73	7,230
Coos-Curry county line	43	690	348	560	222	8.5	72	6,360
Port Orford	61	680	490	590	393	11.1	74	11,980
Port Orford	57	670	548	600	503	12.4	73	13,800

[1] Height of trees of mean basal area.

stands *(13)*. Its slow growth beyond the sapling stage results in its being overtopped, but it continues to grow and retains into old age the ability to respond after the dominants die *(7)*. Port-Orford-cedar can reproduce effectively from seed after clearcutting and partial cutting (where a sufficient seed source is present) and under almost all natural forests, and it can be used for under-planting established forest or scrub *(13)*. Some old-growth forest structures resulted from repeated waves of invasion, almost certainly after fires.

Because of its shade tolerance, relatively thick bark, high value, and moderate but consistent growth rate, Port-Orford-cedar might be grown effectively in a partial-cut system in which faster growing associates are removed part way through the rotation. Its litter (with high calcium and high pH) increases soil pH, suggesting that the species may be important in afforestation of moderately acidic soils or for ameliorating the effects of other conifers on soils *(13)*.

Shade tolerance and a narrow crown allow dense stocking in British plantations, and volume for a given height is high *(13)*. Holes left after thinning close slowly, however, and a longer thinning cycle is necessary than for most conifers. Pruning is not useful. Forking of trees has been a problem in many British plantations.

In recent years, plantations of Port-Orford-cedar have not been widely established in the Pacific Northwest outside its native range because of problems with root rot, winter damage, and its slow growth relative to other species *(13)*.

Damaging Agents—The major causes of damage to Port-Orford-cedar are fungi of the genus *Phytophthora (11,13)*. An exotic root rot caused by *P. lateralis* was introduced into Coos County about 1952 and has decimated many stands in the area where Port-Orford-cedar grows best. Neither resistance to the rot nor effective treatment of it has been identified. Spores of the fungus are carried by water, so one introduction of the disease may spread to all stands in the watershed below. Natural uphill spread is slow. Infections are carried uphill rapidly or between watersheds in mud on equipment or livestock; they have reached northern Del Norte County, CA. Many isolated stands or those uphill from infection centers, however, may be kept free of the disease by careful exclusion of contaminated machinery, livestock, and nursery stock.

Phytophthora cinnamomi causes major losses to some nurseries and cultivated trees. A white pocket top rot, caused by an unidentified fungus, is a serious problem. Losses to other diseases and to insects are minor *(13)*. Animal damage to planted seedlings is highly variable, sometimes more and sometimes less than on associated conifers *(13)*.

Drought damages native trees on the hotter sites and in inland areas without seepage *(13)*. Port-Orford-cedar is more affected than its associates on these sites. Laboratory experiments show that it is also more susceptible to freezing than most associated trees, although reports of winter damage in the field vary *(13)*. In some instances, no damage occurred at -25° *C* (-13° F); others report severe damage at -13° C (9° F). Most drastic winter kill occurred in dry, windy, cold weather, desiccation apparently being of considerable consequence. Susceptibility to spring frosts in Great Britain is lower for Port-Orford-cedar than for most of its usual associates. Damage by wind, ice, and snow occurs, but the species does not seem especially susceptible *(13)*.

Port-Orford-cedar effectively recovers from loss of its leader or from extensive killing of foliage at the crown surface. If twigs are killed deeply enough into the crown, however, a tree apparently does not recover because it does not resprout from the "old wood" *(13)*.

Port-Orford-cedar resists moderate air pollution but does poorly where pollution is intense *(13)*. It is more sensitive to nitrous oxide than nitric oxide. Levels of sulfur dioxide that reduce photosynthesis of Port-Orford-cedar have little effect on Douglas-fir and western redcedar.

Although young trees are easily killed by fire, older trees develop thick bark and survive large, deep fire scars *(13)*. In old stands, Port-Orford-cedar seems as tolerant of fire as Douglas-fir.

Special Uses

Outside its natural range, the major use of Port-Orford-cedar is as an ornamental *(13)*. As such, it is usually referred to as Lawson cypress. More than 200 cultivars are known, varying in size, shape, foliar morphology, and color. It is suitable for hedges but is usually planted as separate individuals of either full-sized or dwarfed varieties. Its use has declined in some areas because of root rot. Cut branches are used in floral arrangements.

Genetics

Population Differences

Port-Orford-cedar is extremely variable morphologically. Most horticultural cultivars originated as seedling mutations, produced by descendants of apparently only a few introductions to Great Britain *(13)*. Some cultivars are notably more resistant to winter damage and spring frosts than are most, and some root more easily than others.

There is obvious variation in growth rates among seedlings and rooted cuttings from various natural populations; northern coastal sources grow faster than those from inland, and those from productive, dense forest types grow faster than those from open forests on poor soils *(13)*. Relative growth rates of different populations remain the same in culture on both good and poor soils. In culture, differences in nutrient content, and stomatal distribution occur among inland and coastal sources, and the foliar calcium-to-magnesium ratio is lower for a source from an ultramafic area than for those from other soils *(13)*. Local variation occurs in stomatal resistance of seedlings to water loss, but it is not consistent regionally.

Variability in adaptation of individual trees has been noted in Europe. Selections of desirable trees have been made in Great Britain. Apparently no provenance studies of growth have ever been made in field conditions *(13)*. Trials of the species as an exotic may have suffered from the use of a limited seed source; the original introduction to Britain was from the upper Sacramento River, probably an area of slow growth.

Allozyme variability differentiated two inland populations from seven coastal populations in California. The disjunct inland populations contained less variability than the coastal samples. Considerable variation among populations existed in both inland and coastal regions *(10)*.

Hybrids

Putative hybrids with *Chamaecyparis nootkatensis* have been identified in cultivation and in a natural sympatric stand *(13)*; apparently none have been confirmed, however.

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Chamaecyparis nootkatensis (D. Don) Spach **Alaska-Cedar**

Cupressaceae **Cypress family**

A. S. Harris

Alaska-cedar *(Chamaecyparis nootkatensis)*, also known as Alaska yellow-cedar, yellow-cedar, Alaska cypress, and Nootka cypress, is an important timber species of northwestern America. It is found along the Pacific coast in Alaska and British Columbia, in the Cascade Range of Oregon and Washington, and at a number of isolated locations *(1,10)*. It is confined to a cool, humid climate. Toward the south, Alaska-cedar rarely grows below 600 m (2,000 ft) in elevation; but north of midcoastal British Columbia, it grows from sea level to tree line. It is one of the slowest growing conifers in the Northwest. The wood is extremely durable and is excellent for specialty uses. Little effort is being made to manage the species to assure a continuing supply.

Habitat

Native Range

Alaska-cedar (fig. 1) grows from northern California to Prince William Sound, AK. Except for a few isolated stands, it is found within 160 km (100 miles) of the Pacific coast. Isolated stands in the Siskiyou Mountains, CA, near the Oregon border mark its southern limit *(2)*. In Oregon and Washington, Alaska-cedar grows in the Cascade Range and Olympic Mountains; scattered populations are found in the Coast Ranges and in the Aldrich Mountains of central Oregon *(8)*. In British Columbia and north to Wells Bay in Prince William Sound, AK, it grows in a narrow strip on the islands and coastal mainland. An exception in British Columbia is an isolated stand near Slocan Lake about 720 km (450 mi) inland.

Climate

Alaska-cedar is notable within the cypress family for its tolerance of cool and wet conditions. The climate of its natural range is cool and humid. Climatic conditions at elevations where Alaska-cedar grows in the Cascade Range of Washington are somewhat comparable to those at sea level in coastal Alaska (table 1). Growing seasons are short.

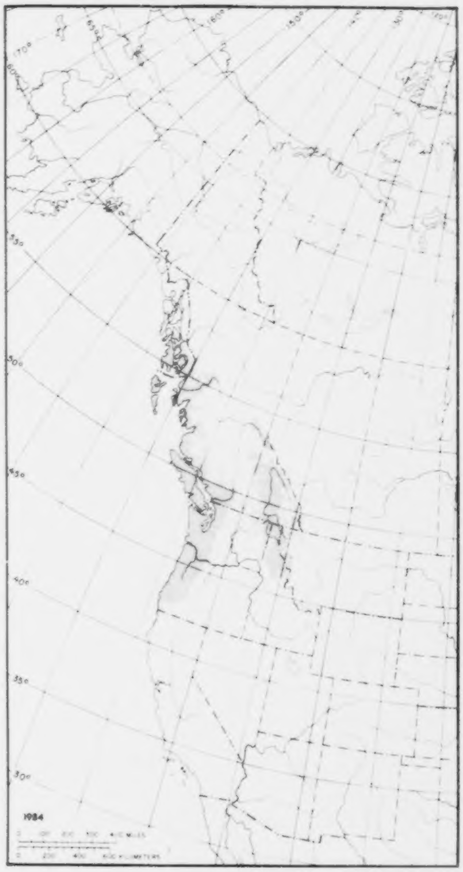

Figure 1—*The native range of Alaska-cedar.*

Soils and Topography

Alaska-cedar grows most commonly on Histosols and Spodosols. Best growth and development are on slopes with deep, well-drained soils. It is seldom found on the better sites, however, because of com-

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petition from faster growing associates. More frequently, it is found on thin organic soils over bedrock and is able to survive and grow on soils that are deficient in nutrients. It grows well on soils rich in calcium and magnesium and frequently on Lithosols developed from andesite, diorite, gabbro, or basaltic rocks *(18)*. It is a common component of "scrub" stands on organic soils at low elevations in Alaska, and on organic subalpine soils. At high elevations and on half-bog sites, it often develops a shrublike or prostrate form.

Alaska-cedar grows at elevations from 600 to 2300 m (2,000 to 7,500 ft) in the Cascade Range in Oregon and Washington and occasionally down to sea level on the Olympic Peninsula in Washington and the west coast of Vancouver Island. In Oregon, most Alaska-cedar grows on ridges and peaks from 1500 to 1700 m (5,000 to 5,600 ft) high in the western Cascades between the Clackamas and McKenzie rivers, but it can grow throughout much of the moisture conditions present at high elevations in the Cascade Range from central Oregon north *(2)*. On the southern British Columbia mainland, it usually grows between 600 and 1500 m (2,000 and 5,000 ft) but is found at lower elevations northward until it reaches sea level at Knight Inlet. From there, north and west to Prince William Sound in Alaska, it is found from sea level to tree line, up to 900 m (3,000 ft) in southeast Alaska and 300 m (1,000 ft) around Prince William Sound.

Table 1—Climate in the range of Alaska-cedar[1]

		Average Annual			
Location	Elevation	Temperature	Precipitation	Snowfall	Frost-free period
	m	°*C*	*mm*	*cm*	*days*
Washington[2]	1206	4	2340	1140	114
Alaska:					
Sitka	4	7	2130	114	149
Cordova	12	5	2260	340	111
	ft	°*F*	*in*	*in*	*days*
Washington[2]	3,958	39	92	450	114
Alaska:					
Sitka	13	45	84	45	149
Cordova	39	41	89	134	111

[1] Compiled from U.S. Weather Service records.

[2] Stampede Pass near Mount Rainier.

Associated Forest Cover

Alaska-cedar occasionally grows in pure stands but is usually found singly or in scattered groups mixed with other tree species. Associated species change with latitude. In California, Alaska-cedar may be found with California red fir *(Abies magnifica)*, Brewer spruce *(Picea breweriana)*, incense-cedar *(Libocedrus decurrens)*, Pacific yew *(Taxus brevifolia)*, and western white pine *(Pinus monticola)*; in Oregon and Washington, with mountain hemlock *(Tsuga mertensiana)*, subalpine fir *(Abies lasiocarpa)*, whitebark pine *(Pinus albicaulis)*, Pacific silver fir *(Abies amabilis)*, noble fir *(Abies procera)*, western white pine, and western hemlock *(Tsuga heterophylla)*; in British Columbia, with Pacific silver fir, western white pine, western redcedar *(Thuja plicata)*, mountain hemlock, western hemlock, and shore pine *(Pinus contorta)*; in Alaska, with western redcedar, western hemlock, mountain hemlock, Sitka spruce *(Picea sitchensis)*, and shore pine.

Alaska-cedar is a component of the following Society of American Foresters forest cover types *(5)*:

205	Mountain Hemlock
223	Sitka Spruce
224	Western Hemlock
225	Western Hemlock–Sitka Spruce
226	Coastal True Fir–Hemlock
227	Western Redcedar–Western Hemlock
228	Western Redcedar

Shrubs commonly associated with Alaska-cedar in Oregon, Washington, and British Columbia are: big whortleberry *(Vaccinium membranaceum)*, ovalleaf whortleberry *(V. ovalifolium)*, Alaska blueberry *(V. alaskaense)*, rustyleaf menziesia *(Menziesia ferruginea)*, Cascades azalea *(Rhododendron albiflorum)*, and copperbush *(Cladothamnus pyroliflorus)*. These shrubs, except *Rhododendron albiflorum* and *Vaccinium membranaceum*, are associates in Alaska as well. Other plant associates include fiveleaf bramble *(Rubus pedatus)*, bunchberry *(Cornus canadensis)*, queenscup *(Clintonia uniflora)*, ferny goldthread *(Coptis asplenifolia)*, deerfern *(Blechnum spicant)*, claspleaf twistedstalk *(Streptopus amplexifolius)*, rosy twistedstalk *(S. roseus)*, and skunkcabbage *(Lysichitum americanum)*.

Recognized vegetative communities from British Columbia south are *Chamaecyparis nootkatensis/ Lysichitum americanum* and *Chamaecyparis nootkatensis/ Rhododendron albiflorum* *(7)*. In southeast Alaska, a common association in the open conifer forest surrounding bogs is *Pinus contorta–Tsuga heterophylla–Thuja plicata–Chamaecyparis nootkatensis/Vaccinium ovalifolium–V. alaskaense–Ledum groenlandicum/Sphagnum squarrosum* *(25)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Alaska-cedar is monoecious. Flowering occurs from April in the southern part of the range to June in the north. The tiny inconspicuous yellow or reddish male pollen-bearing strobili and green female cones are borne on the tips of branchlets. Pollination occurs from mid-April to late May in cones that were initiated the previous summer. Cones generally mature in 2 years, but in the southern part of the range they may mature in 1 year. Both first- and second-year cones occur on the same branch and may easily be confused. Mature cones are about 12 mm (0.5 in) in diameter and globe-shaped (fig. 2). Mature and immature cones are nearly the same size, so care must be taken to collect only mature cones for seed. Immature cones are green and soft, often with purple markings, and are borne near the tips of branchlets. Mature cones are yellow-green and hard, often with brown markings, and are borne farther from the branch tips.

Seed Production and Dissemination—Large crops of Alaska-cedar seed occur at intervals of 4 or more years *(12)*. The proportion of filled seeds from mature cones is generally low and extremely variable. One study in British Columbia showed that the number of seeds per cone averaged 7.2; the proportion of filled seeds was only 29 percent *(21)*. Cleaned seeds average 240,000/kg (109,000/lb) *(12)*. Information is not available on the distance seeds are disseminated by wind. Seeds of Alaska-cedar are heavier than seeds of the closely related Port-Orford-cedar and probably are not disseminated beyond the 120 m (400 ft) reported for that species.

Seedling Development—Germination is epigeal, and the rate tends to be low. Warm stratification followed by cold stratification greatly improves germination, but optimum stratification schedules have not been developed. In British Columbia and Alaska, seeds ripen from mid-September to late September and are shed during dry periods in the fall and early winter. Empty cones remain on trees for 1 year or more.

Formation of both pollen cones and seed cones can be induced in juvenile trees by foliar application of gibberellin-A_3 under conditions of long day length. Cones induced by gibberellin-A_3 yield higher percentages of filled seeds with higher rates of germination than cones that develop under natural conditions. Seed orchards should offer the opportunity for treatment and thereby provide a practical means of increasing cone production *(22)*.

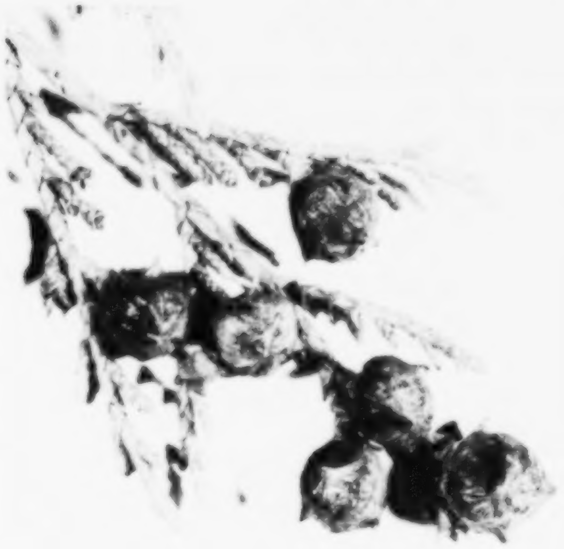

Figure 2—*Mature cones of Alaska-cedar.*

Vegetative Reproduction—Alaska-cedar reproduces vegetatively under a variety of natural conditions from low-elevation bogs to krummholz at tree line *(1,3,20,23)*. In southeast Alaska, layering is common on low-elevation bog sites, less common on better drained sites *(14)*. In contrast, from Mount Rainier, WA, southward to California, layering is most common on drier, high-elevation sites *(2)*. The species can also be reproduced from cuttings. Container stock suitable for planting has been produced in the greenhouse in 1 year by potting young cuttings treated with indolebutyric acid *(17)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Alaska-cedar is slow growing and long lived. In Washington, dominant trees on better sites are typically 30 to 38 m (100 to 125 ft) tall; in British Columbia, they are 90 cm (36 in) in d.b.h. and 23 to 30 m (75 to 100 ft) tall; and in Alaska, dominant trees are often 60 cm (24 in) in d.b.h. and 24 m (80 ft) tall, although larger trees are common (fig. 3). The largest tree on record, located in Olympic National Park, WA, has a d.b.h. of 3.7 m (12.0 ft), a height of 37 m (120 ft), and a crown spread of 8.2 m (27 ft) *(13)*. Growth rates of 16 to 20 rings per centimeter (40 to 50/in) are common. In

Alaska, suppressed trees 15 cm (6 in) in d.b.h. are frequently more than 300 years old; dominant and codominant trees 60 to 90 cm (24 to 36 in) in d.b.h. are from 300 to more than 700 years old. Trees that are extremely old have been reported; a hollow tree 180 cm (70 in) in d.b.h. had 1,040 growth rings in the 30-cm (12-in) outer shell *(1)*.

Rooting Habit—In bogs, roots of prostrate clumps of Alaska-cedar often tend to be shallow and to develop in complex patterns associated with a long history of branch layering *(14)*. Root systems of krummholz Alaska-cedar—apparently the result of root sprouting and layering—have been observed to extend 100 feet *(3)*. Understory trees have shown adventitious rooting the year after partial burial by volcanic tephra *(26)*. Information is not available on the rooting habit of mature trees on well drained sites.

Reaction to Competition—Alaska-cedar is considered tolerant of shade in the southern part of its range but less tolerant toward the north. Overall, it is classed as shade tolerant. South of Mt. Rainier, WA, Alaska-cedar establishes some seedlings and is shade tolerant enough to survive under moderately dense canopies, but forest-grown seedlings fail to develop a strong upright trunk. Most trees on forest sites appear to have been established after disturbance *(2)*. In Alaska, young stands are often even aged, and mixed or nearly pure stands of Alaska-cedar rarely contain seedlings or saplings in the understory. Reproduction of western hemlock is abundant, however, indicating that Alaska-cedar is less tolerant than hemlock *(1)*.

Most Alaska-cedar timber has come from logging mixed old-growth stands in which the species is a minor component. Because of its slow rate of growth in relation to other commercial species, there has been little interest in management of Alaska-cedar for timber on the more productive sites. It may be well suited for planting on cold, wet sites, however, especially at high elevations where other species are less likely to thrive. It survives heavy snow loads because of its narrow, flexible crown and drooping branches, and its flexibility allows it to survive on avalanche tracks. Interest in management of Alaska-cedar is relatively new, and information on growth and yield of young stands is not available. Volume tables are available for old-growth trees *(6)*.

Damaging Agents—Alaska-cedar is relatively free from damage by insects. No infestations of defoliating insects are known *(1)*. Both *Phloeosinus* sp. and the bark-boring, round-headed beetles of the

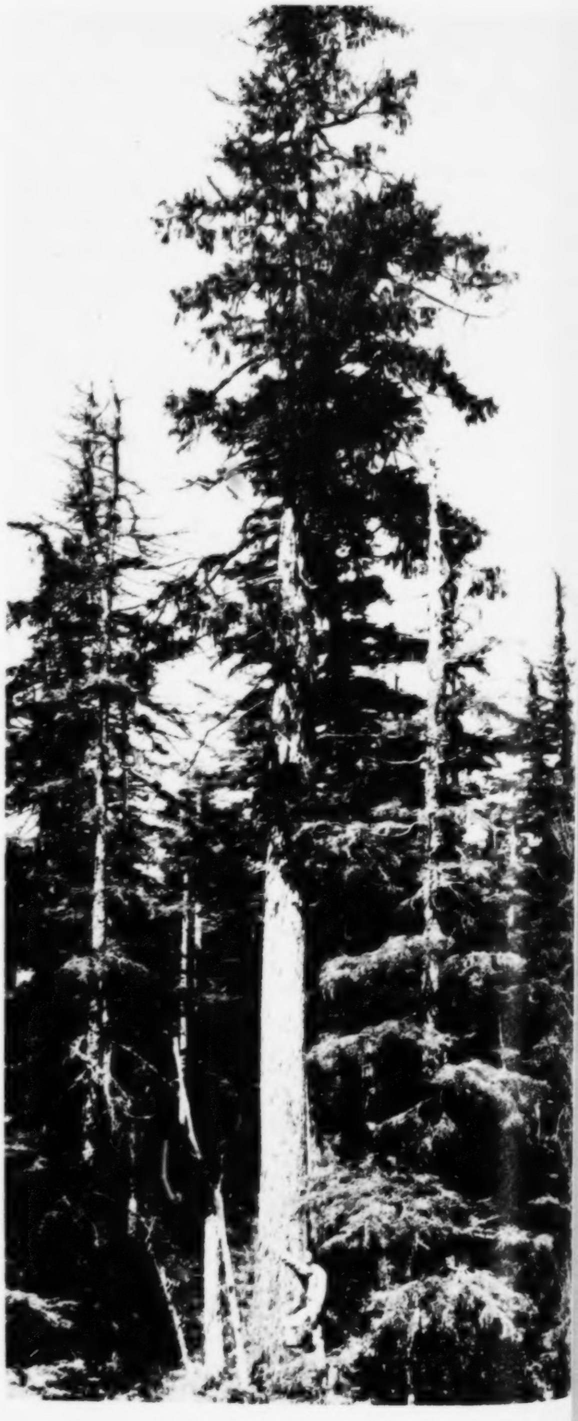

Figure 3—*Old-growth Alaska-cedar, southeast Alaska.*

genus *Atimia* are often found under the bark of dead, dying, or weakened trees and occasionally on healthy trees *(9)*. *Phloeosinus cupressi* is a secondary agent that only attacks trees in advanced stages of decline *(14)*. A total of 78 taxa of fungi have been reported on Alaska-cedar throughout its range, including 50 in Alaska *(14)*. The wood, however, is very durable and resistant to fungal attack, partly because of naturally occurring chemicals—nootkatin, chamic acid, and chaminic acid—in the heartwood that inhibit fungal growth at low concentrations *(4)*. Certain "black-stain" fungi are capable of degrading nootkatin, thereby increasing the susceptibility of the heartwood to decay *(24)*. Living trees often attain great age, and over time heart-rotting fungi cause considerable loss and defect in standing trees *(15)*.

Since at least 1880, Alaska-cedar has suffered advancing decline and mortality on more than 100 000 ha (247,000 acres) of bog and semibog land in southeast Alaska. Abiotic factors appear to be responsible, but the primary cause remains unknown *(14)*.

In southeast Alaska, brown bears *(Ursa arctos)* frequently cause basal scarring by biting and stripping bark. Scarring is most common on well drained sites. This wounding results in fungal attack, which in time reduces volume and value of butt logs *(14)*.

Special Uses

Special attributes of Alaska-cedar wood include durability, freedom from splitting and checking, resistance to acid, smooth-wearing qualities, and excellent characteristics for milling *(11,23)*. It is suitable for boatbuilding, utility poles, heavy flooring, framing, bridge and dock decking, marine piling, window boxes, stadium seats, water and chemical tanks, cooling towers, bedding for heavy machinery, furniture, patterns, molding, sash, doors, paneling, toys, musical instruments, and carving. The wood is highly regarded in Japan, and most high-quality logs are exported.

Genetics

Information on genetic variation of Alaska-cedar is not available *(10)*; however, 15 horticultural varieties of Alaska-cedar are recognized. An intergeneric hybrid, *Cupressocyparis × leylandii (Cupressus macrocarpa × Chamaecyparis nootkatensis)*, has been described in Great Britain *(16)*. This hybrid can be propagated from cuttings and has been planted at numerous locations in temperate regions with good results.

Other intergeneric hybrids include *Cupressocyparis × notabilis* Mitchell *(Cupressus glabra × Chamaecyparis nootkatensis)* and *Cupressocyparis × ovensii (Cupressus lusitanica × Chamaecyparis nootkatensis) (19)*.

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Chamaecyparis thyoides (L.) B.S.P. Atlantic White-Cedar

Cupressaceae Cypress family

Silas Little and Peter W. Garrett

Atlantic white-cedar (*Chamaecyparis thyoides*), also called southern white-cedar, white-cedar, and swamp-cedar, is found most frequently in small dense stands in fresh water swamps and bogs. Heavy cutting for many commercial uses during this century has considerably reduced even the largest stands so that the total volume of this species growing stock is not currently known. It is still considered a commercially important single species in the major supply areas of North and South Carolina, Virginia, and Florida.

Habitat

Native Range

Atlantic white-cedar (fig. 1) grows in a narrow coastal belt 80 to 210 km (50 to 130 miles) wide from southern Maine to northern Florida and west to southern Mississippi. Atlantic white-cedar forests, however, have always been of minor importance because the scarcity of suitable sites makes distribution of the species within the coastal belt exceedingly patchy. White-cedar is most important commercially in southeastern New Jersey, southeastern Virginia, eastern North Carolina, and northwestern Florida (*1,3,8,9,11*).

Climate

The climate throughout most of the range of white-cedar is classed as humid but varies widely in other respects. Average annual precipitation is 1020 to 1630 mm (40 to 64 in) and is well distributed throughout the year. The frost-free season is from 140 to 305 days. Temperature extremes range from -38° C (-36° F) in Maine in winter to highs of over 38° C (100° F) during the summer in most sections (*6*).

Soils and Topography

White-cedar grows on wet ground or in swamps, sometimes on sandy soils, but usually on muck, formerly called peat. Soils include the orders of Spodosols and Histosols. The muck ranges from a few centimeters to 12 m (40 ft) in depth and is generally acid, with pH often between 3.5 and 5.5. White-cedar is absent or uncommon in areas where muck is underlaid by clay or contains appreciable amounts of silt or clay (*6*).

As its range is restricted principally to coastal areas and to wet or swampy ground, Atlantic white-cedar usually grows at low elevation. In southeastern New Jersey these typically range from about 1 m (3 ft), where white-cedars border the tidal marsh, to 43 m (140 ft) in some inland stands. The species currently grows in at least one upland bog in northern New Jersey at an elevation of 457 m (1,500 ft).

Associated Forest Cover

Because Atlantic white-cedar grows characteristically in pure stands it is found mostly in one forest cover type, Atlantic White-Cedar (Society of American Foresters Type 97) (*5*), but is listed as an associate in six other types: Pitch Pine (Type 45); Slash Pine–Hardwood (Type 85); Baldcypress (Type 101); Water Tupelo–Swamp Tupelo (Type 103); Baldcypress–Tupelo (Type 102); Sweetbay–Swamp Tupelo–Redbay (Type104). Over its great latitudinal range, however, several other species of trees have been found growing with it. These include red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), gray birch (*Betula populifolia*), pond pine (*Pinus serotina*), eastern hemlock (*Tsuga canadensis*), and loblolly-bay (*Gordonia lasianthus*).

Many nonarborescent plants also grow with white-cedar. In a study of sixteen 0.04-hectare (0.1-acre) plots in southern New Jersey, the most common species of 25 shrubs associated with it were sweet pepperbush (*Clethra alnifolia*), swamp azalea (*Rhododendron viscosum*), highbush blueberry (*Vaccinium corymbosum*), dangleberry (*Gaylussacia frondosa*), and sweetbells leucothoe (*Leucothoe racemosa*). In a North Carolina study, fetterbush lyonia (*Lyonia lucida*) was the most common shrub, but sweetbells leucothoe, highbush blueberry, and sweet pepperbush were also present (*6*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—White-cedar is monoecious, but the staminate and pistillate flowers are

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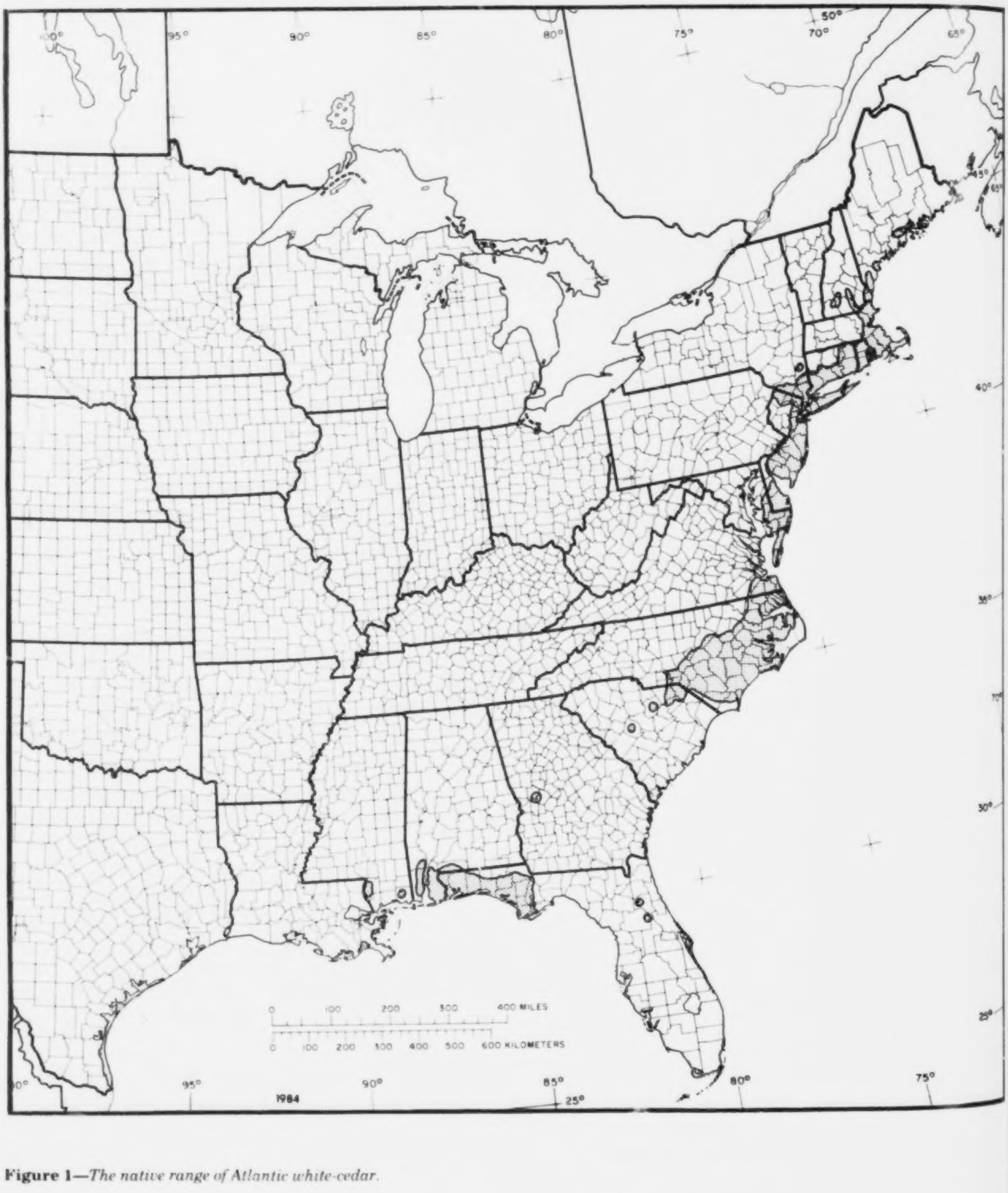
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Figure 1—*The native range of Atlantic white-cedar.*

produced on separate shoots. The flower buds are formed in the summer and, though minute, are discernible in the fall or winter. In New Jersey, the brownish staminate buds are only about 1 mm (0.04 in) long or wide in February. The greenish pistillate buds at the ends of short shoots are about the same size. When mature, the four-sided, oblong, staminate flowers are about 3 mm (0.1 in) long, and the pistillate flowers are about that wide. Pollen shedding usually occurs in early April in southern New Jersey.

The cones mature at the end of the first growing season. Full-grown cones are spherical, about 6 mm (0.2 in) in diameter and contain 5 to 15 winged seeds *(6)*. Seeds are rounded, slightly compressed, about 3 mm (0.1 in) long, and have winged margins about as broad as the seeds. There are about 1,014,000 seeds per kilogram (460,000/lb) *(12)*.

Seed Production and Dissemination—Under favorable conditions, some 3-year-old Atlantic white-cedars bear mature cones. In one planting of 1,300 2-year-old seedlings, 2 percent of the trees had mature cones at the end of the first growing season in the field. In another planting, 20 percent of the 3-year-old seedlings produced one or more cones, and one tree had 64; but these seedlings were relatively large, 28 cm (11 in) tall. Seedlings only 10 cm (4 in) tall produced no cones *(6)*.

Natural reproduction in open stands starts bearing seed at 4 or 5 years, in dense stands at 10 to 20 years *(6)*.

Cone production varies appreciably with tree size and crown class. Intermediate or crowded stems produce markedly fewer cones than open-grown or dominant trees of the same size. In one comparison of clumped and open-grown trees, the larger, mostly dominant trees in the clumps were fully as productive as open-grown trees of the same size; but the intermediate and smaller clumped trees were much less productive than their open-grown counterparts *(4)*. Average numbers of cones per tree for some selected sizes were as follows:

Parent trees	Clumped trees	Open-grown trees
	no. of cones	
1.5 to 2.1 m (5 to 7 ft) tall	4	52
8 to 10 cm (3 to 4 in) d.b.h.	1,074	2,891
13 to 18 cm (5 to 7 in) d.b.h.	4,540	4,218

White-cedar usually produces fair to excellent seed crops each year. Under one mature stand the catch in seed traps was 19.77 million seeds per hectare (8 million/acre) in 1 year and 22.24 million/ha (9 million/acre) the next year *(6)*.

Natural seed dissemination begins in October in New Jersey and most of the seeds are released before the end of the winter. In one study, 39 percent of the crop fell by November 15, more than 60 percent by December 15, and 93 by March 1 *(6)*.

Seed dispersal is influenced by weather conditions. In one series of observations, rain showers of 4 mm (0.16 in) or less caused only partial closing of some cones, whereas rains of 11 mm (0.45 in) or more caused all cones to close *(6)*.

Wind distributes most of the white-cedar seeds, although some may be further scattered by floating on water. Probably because the seeds are so small and have relatively large wings, the rate of fall is slow—0.02 m (0.6 ft) per second in still air. Calculations based on this rate of fall indicate that a wind of 8 km/h (5 mi/h) would carry most seeds from a 15-m (50-ft) tree about 183 m (600 ft). Records of seed traps around and under white-cedar stands showed that most of the seeds fall directly under the stands. Where surrounding vegetation was of comparable height, no seeds were trapped beyond 20 m (66 ft) from the stand's edge.

In a study of seed distribution from isolated trees, 60 percent of the seeds fell at a distance greater than the height of the tree, even though the catch per trap decreased greatly with increased distance. Because of prevailing winds during dry periods, 80 to 85 percent of the seed catch was on the east side of the source *(6)*.

Seedling Development—The viability of white-cedar seeds varies from very low to a high of nearly 90 percent. In some tests, the average was 84 percent *(12)*. One cutting test of New Jersey seeds from a poor crop yielded only 8 percent sound seeds, but actual germination from a good crop the following year reached 76 percent. Viability of seeds from trees 3 to 4 years old may be low; in two tests only 3 to 25 percent of such seeds germinated *(6)*.

Germination is epigeal, but delayed germination is common. Half the seeds sown in the fall in a nursery may not germinate until the second year. Consequently, stratification for 90 days at 4° C (40° F) before sowing has been recommended *(12)*. Some of the seeds produced by mature stands remain viable for an unknown length of time when stored in the forest floor. In a New Jersey study of sites protected from additional seedfall for 1 year, the surface 2.5 cm (1.0 in) of forest floor was found to contain 642,000 to 2,718,000 viable seeds per hectare (260,000 to 1,100,000/acre), with nearly an equal amount in the 5-cm (2-in) muck layer underneath *(6)*.

A fair amount of light is necessary for good germination of white-cedar seeds, but in one study, light intensity had to be less than 16 percent of full sunlight before germination was greatly reduced. Some germination occurred under a hardwood overstory where light intensity was only 1 pecent of full sunlight *(6)*.

Favorable moisture conditions are highly important for the germination and establishment of Atlantic white-cedar seedlings. In one experiment with artificial seeding, 49 percent of the seeds germinated in clearcut plots under typical swamp conditions, whereas in similar plots on drier but still poorly drained sites, only 16 percent germinated on exposed soil. As seedlings develop a very short taproot, the successful establishment of white-cedar requires not only adequate surface moisture for seed germination, but also available moisture within reach of the comparatively shallow root systems.

Suitable seedbeds include moist rotting wood, sphagnum moss, and muck, which are all common in many swamps, and moist mineral soil. A thick litter of pine needles, or the leaves of shrubs and hardwood trees, is unfavorable. On one poorly drained site with a thick litter, removing the litter from seed spots increased germination from less than 1 percent on untreated areas to 13 percent on the cleared spots. Stocking of spots was 3 and 81 percent.

Dense slash is extremely unfavorable for white-cedar establishment. In studies of natural reproduction on cutover areas, slash-free spots had at least 28 times as many seedlings as spots covered with dense slash *(6)*.

The microrelief of swamps also greatly affects seedling establishment. Spots where water stands on the surface during much of the year are unfavorable for both seed germination and seedling survival. Suitable conditions are limited to the hummocks above the usual water table, but on these hummocks seedlings may die during dry periods from insufficient moisture. In general, the younger or smaller the seedlings are, the greater the mortality from either drowning or drought.

Relatively open conditions are essential for good survival and growth of white-cedar seedlings. At light intensities of 4 to 6 percent of full sunlight, as under mature white-cedar stands in New Jersey, seedlings survive for only 1 to 3 years. Partial cuttings that thin the overstory enable white-cedar reproduction to live longer, but not as long as competing hardwoods and shrubs. Under a light intensity of 77 percent, the initial growth of white-cedar seedlings was about twice that under a 16-percent intensity and almost 4 times that under a 2-percent intensity. Hence, only relatively open areas, such as abandoned cranberry bogs and clearcuttings, provide the conditions necessary for white-cedar seedlings to compete successfully with hardwood and shrub associates *(6)*.

Open-grown Atlantic white-cedar seedlings may reach an average height of 6 cm (2.5 in) on unfavorable sites (such as sandy, poorly drained soils or cranberry bogs) and 15 to 25 cm (6 to 10 in) on favorable sites in the first year. In contrast, seedlings growing in swamps under heavy shade may reach a height of only 2.5 cm (1 in) and a taproot length of only 5 cm (2 in) during the same time.

On favorable open sites, seedlings add 0.2 to 0.3 m (0.6 to 0.9 ft) to their height during the second year, and about 0.3 m (1 ft) a year for a few years thereafter. Under these conditions, stems 3 m (10 ft) tall may be 7 or 8 years old in the South and about 10 years old in the Northeast. On less favorable sites, however, they may grow to heights of only 1.2 to 2.1 m (4 to 7 ft) in 15 years *(6)*.

Vegetative Reproduction—White-cedar seedlings or saplings, if severely browsed or otherwise injured, will sometimes develop shoots from lateral branches or from dormant buds on the stem. One white-cedar seedling girdled by meadow mice produced 26 sprouts 2 to 10 cm (1 to 4 in) long at its base. Seedlings of this species when repeatedly browsed by deer may develop multiple stems through layering. From one such seedling 1 m (3 ft) tall, 14 additional stems 0.2 to 1.0 m (0.5 to 3.3 ft) tall developed. Growth of the layered stems is slow, however *(6)*.

Sapling and Pole Stages to Maturity

Growth and Yield—On good sites white-cedar grows 0.3 to 0.5 m (1.0 to 1.5 ft) in height each year and 0.25 to 0.40 cm (0.10 to 0.15 in) in d.b.h. until trees are 40 to 50 years old. After 50 years, height growth slows, while diameter growth continues at about the same rate for an additional 50 years. Height growth essentially ceases at 100 years *(6)*.

Although white-cedar trees are relatively small, the basal area and volume of stands tend to be high because of the high stand density. On the basis of three 0.1 ha (0.25 acre) plots, one stand in Gates County, NC, had 68 m^2/ha (294 ft^2/acre) of basal area, 85 percent of which was white-cedar. Most of the trees of these plots were between 5 and 36 cm (2 and 14 in) in d.b.h. According to yield tables, basal areas may reach more than 69 m^2/ha (300 ft^2/acre). On areas with a site index at base age 50 years of 14 m (45 ft), 50-year-old stands may have 56 to 57 m^2/ha (245 to 250 ft^2/acre) of basal area and a total volume, including stumps and tops, of 322 m^3/ha (4,600 ft^3/acre). On a site index of 12 m (40 ft), a 60-year-old stand may have 4,200 stems per hectare (1,700/acre), yielding about 220 m^3/ha (35 cords/acre) to an inside-

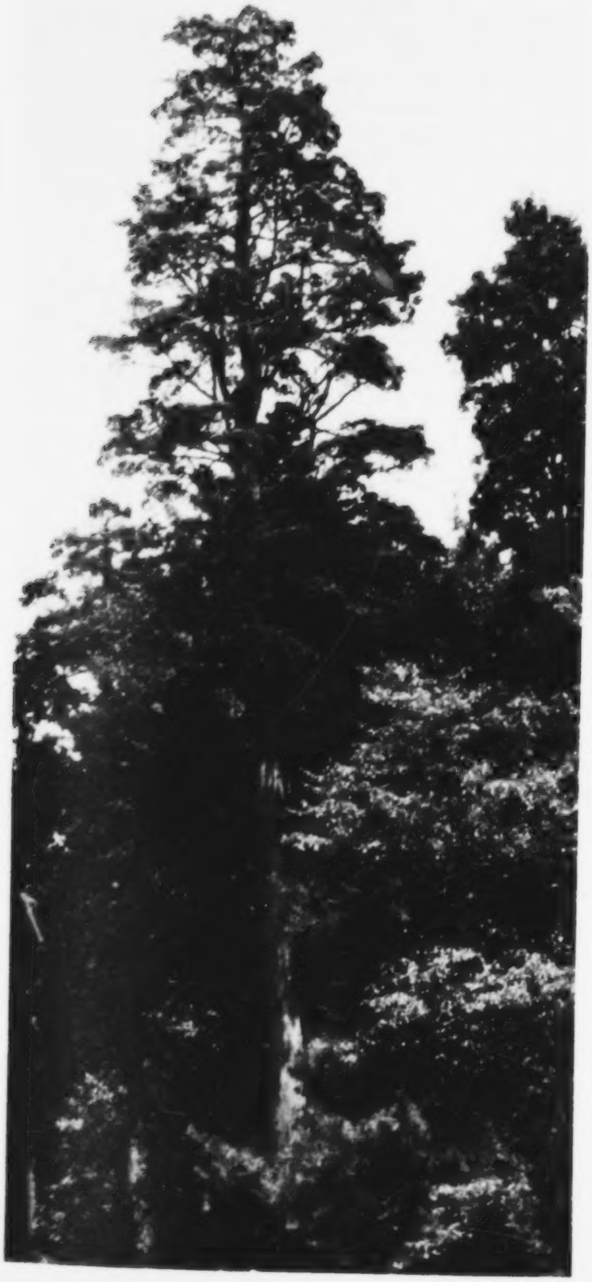

Figure 2—*Atlantic white-cedar on Lebanon Experimental Forest, NJ.*

bark top diameter of 10 cm (4 in); a 70-year-old stand on a site index of 21 m (70 ft), 865 trees per hectare (350/acre) and 693 m^3/ha (110 cords/acre). The yield to an inside-bark top diameter of 15 cm (6 in) is 600 m^3/ha (42,900 fbm/acre, International rule) at 60 years, and 1000 m^3/ha (71,500 fbm/acre) at 100 years, both on a site index of 21 m (70 ft) *(6)*.

In southern New England (lat. 41° to 42° N.), mature white-cedars (fig. 2) reach heights of 12 to 18 m (40 to 60 ft) and a d.b.h. of about 41 cm (16 in), although some have grown to 122 cm (48 in). Optimum development—a maximum height of 37 m (120 ft) and a d.b.h. of 152 cm (60 in)—apparently occurred in the Virginia–North Carolina section at lat. 34° to 37° N. The maximum sizes for white-cedar in Alabama (approximately lat. 31° N.) are somewhat less: 24 to 27 m (80 to 90 ft) high, with d.b.h. rarely more than 61 cm (24 in) *(6)*.

Potentially, white-cedar is a relatively long-lived species. According to one source, some trees have reached 1,000 years of age, although stand age rarely exceeds 200 years *(6)*.

Rooting Habit—Atlantic white-cedar has a shallow root system. In swamps where the lower soil layers are permanently saturated with water, the roots are confined chiefly to the upper 1 to 2 feet of peat. Where the water table occurs at lower levels and the soils are more deeply aerated, the roots often penetrate to greater depths.

The small taproot formed during the first year is subsequently lost in the development of the strong superficial lateral roots. These are numerous but do not become large. Because of its characteristically shallow root system and weak root hold in the spongy organic soils, white-cedar cannot withstand severe winds, and many mature trees are felled in storms. Trees which have grown in dense stands on swamp peat never become windfirm, and consideration must be given this fact in planning the harvest of this species.

Reaction to Competition—Atlantic white-cedar is more tolerant of shade than associated species such as gray birch and pitch pine, but much less tolerant than red maple, blackgum, sweetbay, and other hardwoods that form the climax on swamp sites in its range. It is most accurately classed as intermediate in tolerance to shade. White-cedar reproduction can grow through, and eventually overtop, scattered to moderately dense shrubs such as highbush blueberry, although in the process the cedar shoots may become extremely slender, almost like grass. White-cedar is not sufficiently tolerant, however, to grow through dense shrub thickets or through a hardwood overstory *(6)*.

Damaging Agents—Crown fires kill white-cedar. Composition of the succeeding stand varies according to (1) the degree to which the forest floor is burned, (2) the age of the burned stand and thus the amount of viable seed stored in the forest floor, (3) the proximity to other sources of white-cedar seed, and (4) the stocking of hardwoods and shrubs in the understory. If fire burns deep enough to eliminate trees of all kinds, a pond (or open bog) or a cover of leatherleaf *(Chamaedaphne calyculata)* may result. If the hummocks remain above the water table, a new stand of Atlantic white-cedar or hardwoods usually develops.

White-cedar on typical swamp sites is shallow rooted and subject to windthrow, especially in stands that have been opened by partial cuttings. Wind, often aided by snow or ice, is beneficial to hardwood understory development at times when white-cedar stands are gradually opened by the periodic windthrow or breakage of scattered trees; but extensive wind damage in one storm favors development of another white-cedar stand. Along the coast, salt water brought in by storm tides kills stands of various species, sometimes permitting a pure white-cedar stand (developing from seeds stored in the forest floor) to follow one composed largely of hardwoods *(6)*.

Few fungi attack Atlantic white-cedar, and damage is not usually serious. *Keithia chamaecyparissi* and *Lophodermium juniperinum* attack white-cedar foliage; *Gymnosporangium ellisii* sometimes causes a broomlike development of branches; *G. biseptatum* occasionally causes a spindle-shaped swelling of stems or branches. Roots may be attacked by *Armillaria mellea*, *Heterobasidion annosum*, or *Phaeolus schweinitzii*. The latter and *Fomitopsis cajanderi* may attack heartwood, although the heartwood of Atlantic white-cedar is very resistant to decay *(7)*.

White-cedar has no serious insect enemies, although larvae of the common bagworm *(Thyridopteryx ephemeraeformis)* may feed on its foliage.

Special Uses

The lightweight, straight-grained wood of Atlantic white-cedar is easily worked, resistant to decay, and shrinks and warps very little during seasoning. These characteristics probably govern its use today as much as they did in colonial times. In those times it was used for shingles, barrels, tanks, and small boats. Today it is still used where durability, light weight, and resistance to weathering are important considerations: telephone poles, piling, ties, siding, boat railing, and ice cream tubs. Atlantic white-cedar has limited value for wildlife—white-tailed deer browse its foliage—and is occasionally used as an ornamental *(2,4)*.

Genetics

In some taxonomic treatments of white-cedar, the southern element in Florida, Alabama, and Mississippi has been named as a separate variety, *Chamaecyparis thyoides* var. *henryae* (Li) Little. Of the many horticultural cultivars, at least one narrow, upright form has been described *(10)*.

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Juniperus occidentalis Hook. Western Juniper

Cupressaceae Cypress family

J. Edward Dealy

Western juniper *(Juniperus occidentalis)* is also called Sierra juniper. There are two subspecies separated geographically, *occidentalis* in the northern part and *australis* in the southern part of its range. Unless specifically identified, both are included in the following discussion. One of the largest western junipers recorded grows on the Stanislaus National Forest in California. It measures 414 cm (163 in) in d.b.h., is 26.5 m (87 ft) tall, and has a crown spread of 15.5 m (51 ft).

Habitat

Native Range

Western juniper (fig. 1) is found intermittently from latitude 34° N. in California to latitude 46° 37′ N. in southeastern Washington, in a narrow belt from longitude 117° W. in Idaho and California to longitude 123° W. in northern California, and in sparse, scattered stands in south-central and southeastern Washington, southeastern Oregon, and the northwest corner of Nevada. In southwestern Idaho, it grows on approximately 162 000 ha (400,000 acres) *(2)*. Western juniper reaches its greatest abundance as extensive and continuous stands in central Oregon. Stands more limited in size extend up the valleys and foothills of the southern Blue Mountain region, and small groups or individuals are scattered sparsely through the northern Blue Mountains. Extensive stands are common on the plains and in the foothills of north-central Oregon, and large stands occur down the high plains and foothills of south-central Oregon *(5,6)*. From north-central through south-central Oregon, western juniper grows in various densities on roughly 1 140 000 ha (2,816,000 acres) *(5)*. It is found near Mount Ashland in southwestern Oregon *(10)*, the only native stand documented west of the Cascade Range in Oregon. It grows in scattered locations west of the Cascades in northern California and extends south to Trinity County. Western juniper is present in extensive stands from the Oregon border south through the Pit River Valley in northeastern California and continues intermittently as sparse stands in a narrow corridor along eastern California south to disjunct stands in the San Bernardino Mountains *(17)*. The eastern limits of this species are in San Bernardino County, CA, and Owyhee County, ID. The western limit is Trinity County, CA.

Climate

Northern populations of western juniper grow in a climate characterized as continental. The climate is semiarid with typical intermountain characteristics of dry hot summers, cold winters, and precipitation of 230 to 355 mm (9 to 14 in), which occurs principally as snow during the winter and as rain in the spring and fall *(5)*. Precipitation is generally sparse in the summer. Frost can occur during any month in central Oregon, the area of western juniper's most extensive stands; however, July and August are generally frost free. Temperatures in central Oregon range from a record low of -32° C (-26° F) during January to a record high of 41°C (105° F) during August. The average temperature in January is -1° C (30° F) and in July, 18° C (64° F). Southern populations of western juniper grow in a similar climate; however, winter temperatures are less extreme than in northern areas. Summer lightning storms are common in the western juniper zone and result in natural fires which have historically had a major influence on distribution and past occurrence of juniper.

Although western juniper grows in extensive stands in a narrow range of precipitation (230 to 355 mm; 9 to 14 in) in central Oregon, it is a minor species in many upper elevation areas of higher precipitation. The latter areas have shallow, rocky soils too droughty to support other more common upper-slope conifers.

Soils and Topography

Western juniper grows on soils developed in parent materials originating from metamorphic, sedimentary, and igneous sources. Included are tuff, welded tuff, pumice, volcanic ash, rhyolite, andesite, granite, basalt, and eolian soils, and colluvial or alluvial mixtures of these soils. Western juniper forms complex patterns on zonal, intrazonal, and azonal soils. Profile development is often weak. Soils are generally stony but can be nearly free of stones. They are commonly shallow (25 to 38 cm; 10 to 15 in) but range to deep (more than 122 cm or 48 in). Fractured bedrock or broken indurated subsoil layers commonly occur under shallow overburdened soils. Surface

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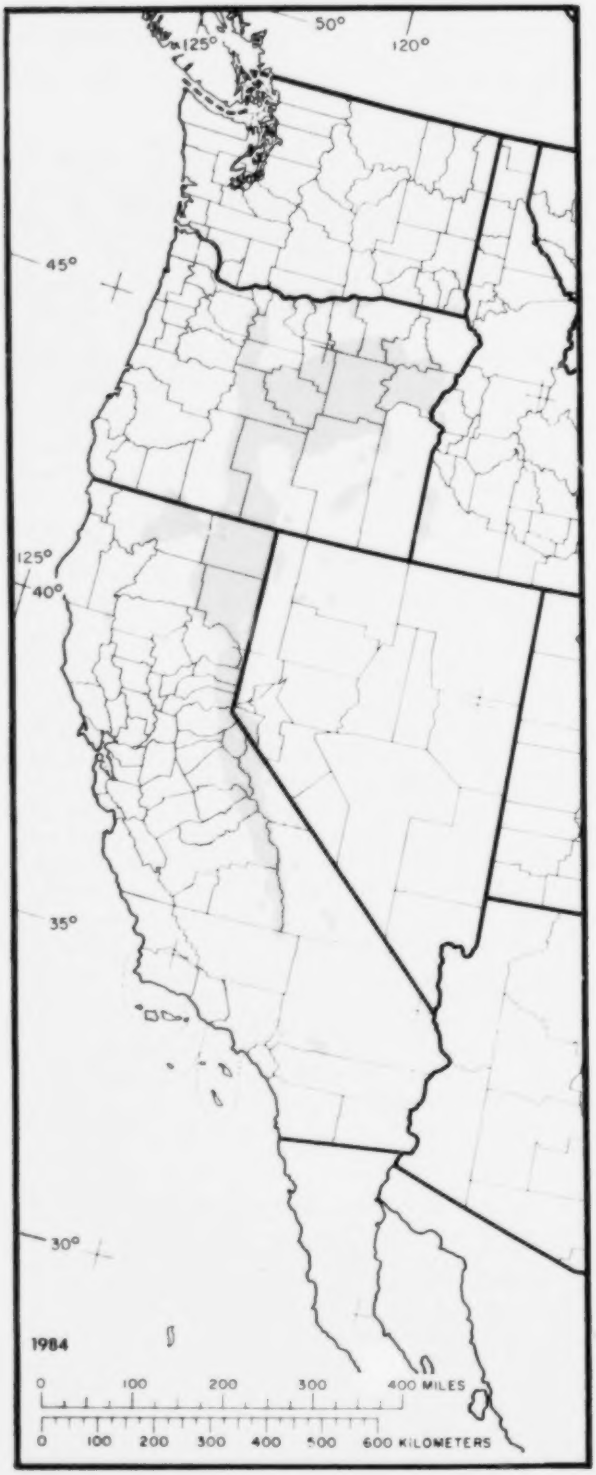

Figure 1—*The native range of western juniper.*

horizons are often of medium texture, and subsoils of medium to fine texture; however, textures can vary from sandy to clayey. Indurated layers can occur and are associated with accumulations of clay, calcium carbonate, and silica. They may be less than 1.5 cm (0.6 in) to several centimeters thick *(5,6,8)*.

Under mature western juniper trees in central Oregon, soil Ca, K, and pH are higher than in interspace soils and soils under young trees. These changes appear to increase the ability of western juniper to compete with other vegetation *(7)*.

Soils supporting juniper at high densities are frequently Mollisols. Argixerolls, Haploxerolls, and Haplaquolls are common great groups. Soils supporting scattered juniper are commonly Aridisols—including Camborthids, Durargids, and Haplargids; however, Argixerolls are also common. Other soils on which western juniper can be found are Durixerolls and Cryoborolls of the order Mollisols, Torriorthents of the order Entisols, and Chromoxererts of the order Vertisols *(5,6)*.

Western juniper is found on all exposures and slopes. In central Oregon, it is common in large continuous stands on level to gentle topography. In other areas, it grows less continuously on terraces, moderately sloping alluvial fans, canyon slopes, and steep, rocky escarpments *(5,6,8)*. Elevations at which western juniper is found range from about 185 m (600 ft) along the Columbia River to more than 3050 m (10,000 ft) in the Sierra Nevada *(24)*. In central Oregon, there are large, continuous stands between 670 and 1525 m (2,200 and 5,000 ft) *(8)*.

Associated Forest Cover

Western juniper is a single species overstory in many northern stands. In ecotones or transitions, ponderosa pine *(Pinus ponderosa)* and curlleaf mountain-mahogany *(Cercocarpus ledifolius)* are the most common tree associates at the lower edge of the conifer zone *(5,6)*. At upper elevations, western juniper often grows in narrow ecotones where deep, forested soils grade into shallow, rocky scab flats. Small stands or groups of trees commonly grow where rock outcrops produce shallow soil inclusions in ponderosa pine, Douglas-fir *(Pseudotsuga menziesii)*, white fir *(Abies concolor)*, lodgepole pine *(Pinus contorta)*, and other forest types *(5,6,11)*. In the Sierra Nevada, western juniper may be found on shallow soils with Jeffrey pine *(Pinus jeffreyi)*, California red fir *(Abies magnifica)*, whitebark pine *(Pinus albicaulis)*, mountain hemlock *(Tsuga mertensiana)*, or lodgepole pine *(24)*. At the southern extension of its range in San

Bernardino County, it generally grows at a higher elevation than California juniper (*Juniperus californica*) and Utah juniper (*J. osteosperma*) (*20*). This is the only documented area where western juniper and singleleaf pinyon (*Pinus monophylla*) grow together in a pinyon–juniper woodland vegetation type, although distributions are known to overlap geographically near the west edge of Nevada and from east-central to southern California (*10,13*). Western juniper is the associate of singleleaf pinyon only in the high altitude section of the type, primarily near Big Bear Lake, CA (*13*).

Western juniper is recognized in five forest cover types (*9*). It is the dominant species in Western Juniper (Society of American Foresters Type 238); an associate species in Interior Ponderosa Pine (Type 237) and Jeffrey Pine (Type 247); and a minor or occasional species in Blue Oak–Digger Pine (Type 250) and California Mixed Subalpine (Type 256).

Big sagebrush (*Artemisia tridentata*) is the most common shrub species associated with western juniper throughout its range. Other shrubs common to western juniper communities in the northern portion of its range are gray rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidiflorus*), antelope-brush (*Purshia tridentata*), wax currant (*Ribes cereum*), and horsebrush (*Tetradymia* spp.). Less common shrubs are low sagebrush (*Artemisia arbuscula*), stiff sagebrush (*A. rigida*), spiny hopsage (*Atriplex spinosa*), broom snakeweed (*Gutierrezia sarothrae*), prickly phlox (*Leptodactylon pungens*), and desert gooseberry (*Ribes velutinum*) (*2,5,8*).

Common grass or grasslike species in northern areas are bluebunch wheatgrass (*Agropyron spicatum*), cheatgrass (*Bromus tectorum*), Idaho fescue (*Festuca idahoensis*), prairie Junegrass (*Koeleria cristata*), Sandberg bluegrass (*Poa sandbergii*), bottlebrush squirreltail (*Sitanion hystrix*), and Thurber needlegrass (*Stipa thurberiana*). Less common are threadleaf sedge (*Carex filifolia*), Ross sedge (*C. rossii*), sixweeks fescue (*Festuca octoflora*), needle-andthread (*Stipa comata*), and western needlegrass (*S. occidentalis*). Forb species common to northern communities include western yarrow (*Achillea millefolium*), milkvetch (*Astragalus* spp.), littleflower collinsia (*Collinsia parviflora*), obscure cryptantha (*Cryptantha ambigua*), lineleaf fleabane (*Erigeron linearis*), woolly eriophyllum (*Eriophyllum lanatum*), spreading groundsmoke (*Gayophytum diffusum*), lupine (*Lupinus* spp.), a suffrutescent wild buckwheat (*Eriogonum* spp.), and tufted phlox (*Phlox caespitosa*). Less common associates are sulfur eriogonum (*Eriogonum umbellatum*), small bluebells (*Mertensia longiflora*), and Hooker silene (*Silene hookeri*) (*2,5,8*).

Major western juniper associations in central Oregon include Juniperus/Artemisia/Festuca, Juniperus/Artemisia/Festuca–Lupinus, Juniperus/Festuca, Juniperus/Artemisia/Agropyron–Chaenactis, Juniperus/Artemisia/Agropyron, Juniperus/Artemisia/Agropyron–Astragalus, Juniperus/Artemisia–Purshia, Juniperus/Agropyron, and Juniperus/Agropyron–Festuca (8).

In one treatment of vegetation types in the conterminous United States, western juniper is considered the dominant species in the Juniper Steppe Woodland (*Juniperus–Artemisia–Agropyron*), number 24, and is a secondary species in the Juniper–Pinyon Woodland (*Juniperus–Pinus*), number 23 (*8,10,17*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—The northern *Juniperus occidentalis* ssp. *occidentalis* is submonoecious; the southern subspecies *australis* is dioecious.

In Oregon and Washington, western juniper flowers in spring and sheds pollen in May. Yellowish-brown staminate cones are terminal, ovoid, and 3 to 4 mm (0.12 to 0.16 in) long. They have 12 to 15 microsporophylls. Ovulate cones are 6 to 8 mm (0.24 to 0.31 in) long, subglobose to ellipsoid, bluish-black when mature, and very glaucous. Ovulate cones, referred to as berries, have resinous pulp and mature in September of the second season in Oregon, Washington, and Idaho. Ovulate cones commonly have two to three developed seeds, rarely one. The seed has a thick, bony outer coat and a thin, membranous inner coat. The membranous coat surrounds a fleshy endosperm within which a straight embryo with cotyledons occurs (*4,14,24,26*).

Seed Production and Dissemination—Good seed production in western juniper occurs nearly every year. Seed yield from 45 kg (100 lb) of fruit averages 9 kg (20 lb). Cleaned seeds average 27 000/kg (12,300/lb) and range from 17 600 to 35 000/kg (8,000 to 15,860/lb) (14).

Seeds are disseminated during the fall, primarily by birds and mammals. Animals ingest the fruit but do not digest the seeds. Dissemination of seeds by animals is evidenced by seed-filled droppings, particularly from robins and coyotes. Western juniper is often found growing along fence rows, seeds having been deposited there by perched birds (*14,19,24*).

Fruit can be collected after it has fallen from the tree or by handpicking it from the tree. Care must be taken when collecting fruit directly from the tree because the new, unripe crop and the 2-year-old, ripe crop are mixed. Fruit should be collected as soon after ripening as possible to prevent removal by animals. It should be stored in shallow trays or piles to prevent excessive heating until seeds are extracted.

Seeds of western juniper may be extracted from fruit by use of a macerator or hammermill in conjunction with water. Because of its resinous nature, pulp is more easily removed from the seeds if berries are presoaked in a lye solution consisting of 1.25 grams of sodium hydroxide or potassium hydroxide per liter (1 teaspoon to 1 gallon) of water for 1 to 2 days. After they are cleaned, seeds should be washed to remove the lye and then stored dry in sealed containers at -2° to 4° C (29° to 40° F) and with a moisture content of approximately 10 percent *(14)*.

Seedling Development—Natural germination of western juniper occurs during April in Oregon. Germination is epigeal. How long after fruit ripening germination occurs and what dormancy characteristics are present are not known. Seeds of many juniper species show delayed germination because of dormant embryos or hard seed coats. Seeds of western juniper are thought to have both these characteristics. Stratification of seeds should be conducted in a sand or peat medium. A warm stratification is suggested for western juniper, fluctuating from 20° C (68° F) at night to 27° C (81° F) during the day for 45 to 90 days, and then cold stratification of approximately 4° C (39° F) to induce germination *(14)*. After stratification, seeds can be sown in the fall or spring. For spring planting, seeds should be sown before air temperatures reach 21° C (70° F).

Bare mineral soil seedbeds are reported as best for successful germination of seed and establishment of seedlings *(24)*. Young plants are normally vigorous, single stemmed, and have pyramidal forms.

Western juniper is very hardy in the early growth stage, resists disease and insect attacks well, and is not preferred as a food item by domestic or wild animals. Considerable browsing, however, occurs on deer winter ranges when other forage is limited; heavy use results in a hedged growth form.

Vegetative Reproduction—Planting stock has been successfully grafted and cuttings have been successfully rooted in experimental trials. Some stock has been developed by layering *(24)*.

Sapling and Pole Stages to Maturity

Growth and Yield—In the sapling and pole stages, western juniper (fig. 2) has straight boles, and the crown varies from medium tapered to round. Early growth rate varies by site; however, growth throughout its range is poor, relative to most conifer species.

Height of mature trees ranges from 4 to 10 m (13 to 33 ft), with exceptions at both ends of the spectrum, depending on site conditions. Occasionally, trees reach exceptional heights, such as one recorded as 26.5 m (87 ft) tall and 396 cm (156 in) in d.b.h.; and another, 26.5 m (87 ft) tall and 414 cm (163 in) in d.b.h. *(4,21)*. Boles of mature trees are massive and more tapered than those of many conifer species, and the butt section is often slightly fluted. This species commonly develops full crowns and heavy limbs at maturity and, in the overmature stage, has a ragged, dead-topped, gnarled appearance. Western juniper is a long-lived and ruggedly picturesque species, reaching ages estimated to be more than 1,000 years *(24)*. Old-growth stands in central Oregon are between 200 and 400 years old.

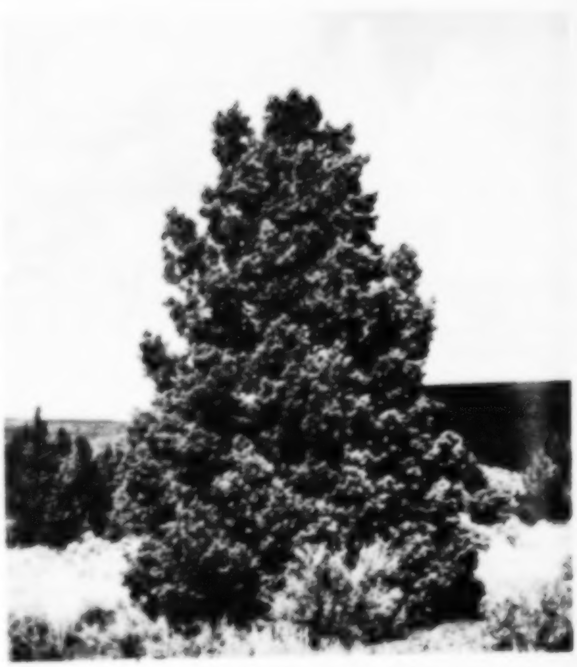

Figure 2—*A mature western juniper tree.*

Rooting Habit—Seedlings of western juniper, typical of arid site species, produce rapid spring root extension with minimal top growth. There is a greater downward growth than lateral growth of roots, again characteristic of arid site species. As seedlings become established, their roots extend laterally to take maximum advantage of nutrients and seasonal moisture in upper soil horizons. As a mature tree, western juniper lacks a central taproot. It has roots that are wide spreading and strong, often penetrating deep into cracks of bedrock.

Reaction to Competition—Western juniper is intolerant of shade and competes poorly with conifers on upper slope sites. Although many individual specimens are found growing as seedlings or saplings in upper slope conifer communities with moderate to dense crowns, they are usually small and suppressed and have low vigor. Establishment of western juniper in this situation apparently occurs when the stand is opened by disturbance.

Western juniper is intolerant of fire and historically was kept in restricted sites by natural fires. Since the advent of effective fire control and intensive livestock grazing (reducing ground fuel and understory competition), regeneration and establishment of western juniper have expanded into suitable sites previously dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). This expansion of young stands is common in Oregon, Idaho, and northeastern California *(2,3,5,6)*.

Damaging Agents—Because of the characteristic wide spacing in most stands, the short stature of the trees, and the extensive, strong root systems that often penetrate cracked rock under the soil mantle, western juniper is very resistant to wind. Most damage from wind occurs as top breakage in mature and overmature trees, and little damage occurs in young stands. Fire resistance varies with age. Seedlings, saplings, and poles are highly vulnerable to fire *(18)*. Mature trees have some resistance to fire because they have little fuel near the stem and relatively thick bark, and because foliage is fairly high above the ground. Old-growth stands remain in existence because, historically, intense natural fires have not occurred and human-caused fires have been controlled *(2,3,5,6)*. Because of effective fire controls, young stands are expanding into shrublands that would otherwise be maintained by periodic natural fires (fig. 3) *(2)*. Where desired, it is easiest to control or eliminate western juniper on rangelands with fire management when trees are less than 2 m (6 ft) tall. The taller the trees become, the more intense the fire must be to obtain good control. If a site has developed a dense stand of large trees, fuel consisting of shrubs and bunchgrass is often inadequate for burning trees under any weather conditions that management can safely tolerate *(18)*.

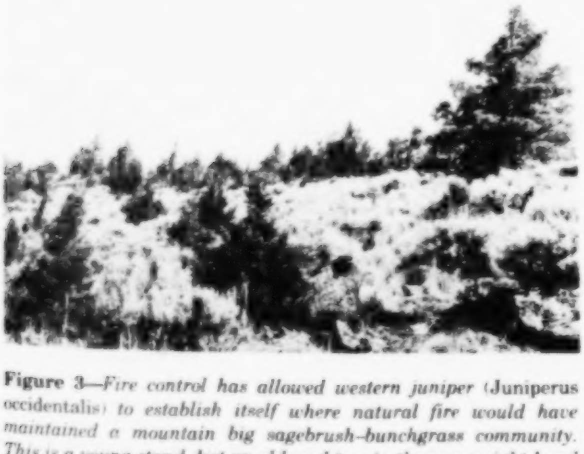

Figure 3—*Fire control has allowed western juniper* (Juniperus occidentalis) *to establish itself where natural fire would have maintained a mountain big sagebrush–bunchgrass community. This is a young stand, but an old seed tree in the upper right-hand corner has escaped previous fires.*

Because the species has relatively little commercial value, little attention has been given to the identification or effect of insects that attack western juniper. Serious damage in western juniper by insects is infrequent. The juniper bark beetle (*Phloeosinus serratus*) can cause mortality, particularly to trees in a weakened condition, during a drought *(24)*. Gall midges feed on western juniper and produce galls; however, their effect on productivity has not been studied. Although termites are not considered a problem in use of products made from western juniper wood, an unidentified species of termite has been observed in dead material on lower portions of overmature trees, as well as in juniper fenceposts in central Oregon.

The principal damaging agents to western juniper are a white trunk rot (*Pyrofomes demidoffii*) that attacks living trees and an unidentified brown cubicle rot usually found in the basal portions of the trunk *(24)*. These rots cause high losses and have prevented the use of western juniper wood for pencils. A single sporophore in evidence usually indicates a tree is unmerchantable. The endophytic fungi *Retinocyclus abietis anamorpha* and *Hormoneme* sp. have been found on the foliage of western juniper. Infection rates increase with age, density, and purity of stands. In general, western juniper is minimally susceptible to infection *(22)*. Two mistletoes, identified as constricted mistletoe (*Phoradendron ligatum*) and dense mistletoe (*P. densom*), cause lower vigor, deformity of branches, and brooming of the foliage *(12)*. A third mistletoe, *P. juniperinum* (Viscaceae), also occurs on western juniper *(25)*. Brooming of foliage is also caused by the stem rusts *Gymnosporangium kernianum* and *G. betheli*. One other rust of the same genus has been reported *(12)*. Except for the white trunk rot and the unidentified brown one, none of the diseases that attack western juniper has been assessed.

Special Uses

Western juniper has had no widespread commercial value. During the pioneer era, it was important as firewood and as poles for fences, corrals, and simple shelters. Locally, it is still important for many of the same uses *(5)*. Heartwood is extremely durable and far outlasts other local materials in northern areas when placed in contact with the ground. It probably equals durability of other junipers and of cedars in more southern areas.

Western juniper logs are difficult to process. They are rough, limby, short, and have rapid taper. They also have bark inclusions deep in the wood. Juniper is reputed to be difficult to cure because it twists and warps while drying, and to be difficult to plane, splitting easily. The reputation is undeserved–local specialty manufacturers have been air-drying this wood successfully for many years *(12)*. Thin boards can be kiln-dried successfully without checking. In fact, any slow drying process works well. Local manufacturers use western juniper for making furniture, novelty items, toys, tongue-and-groove interior paneling, fenceposts, and firewood. Products experimentally manufactured that are considered commercially feasible include hardboard, particle board, veneer, and exposed and decorative interior studs. Research in extracted essential oils indicates that cedrol, used in scenting and flavoring, could be extracted in quantities and would be of a quality to be commercially competitive with cedrol from other juniper species *(1,12)*.

Western juniper is valuable for wildlife cover, food (primarily berries), and nest sites, and as shade for livestock *(16,19)*. Also, management agencies use harvested trees as riprap for stabilizing streambanks. Natural stands in developing areas are highly valuable for landscaping homesites, but the species has not been popular for horticultural uses.

Genetics

Two subspecies of western juniper have been identified, *Juniperus occidentalis* ssp. *occidentalis* and ssp. *australis*. Distribution of the former is in south-central and southeastern Washington, eastern Oregon, southwestern Idaho, northeastern California, and the northwestern corner of Nevada; that of the latter is near Susanville in Lassen County, CA, south to San Bernardino County, CA *(4,10,20,23,26)*. The only other divergence reported is a variant that has a narrow spirelike habit and occurs in a very restricted location in central Oregon *(24)*.

Western juniper may be hybridizing with Utah juniper where the two species grow together in northwestern Nevada east of California's Warner Mountains. Two relict individuals in the White Mountains of California may be hybrids of western juniper and Utah juniper *(26)*.

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Juniperus scopulorum Sarg. Rocky Mountain Juniper

Cupressaceae Cypress family

Daniel L. Noble

Rocky Mountain juniper (*Juniperus scopulorum*) is one of 13 junipers native to North America. It is similar to eastern redcedar (*Juniperus virginiana*) but requires 2 years for seed maturity, compared to 1 year for its eastern relative. Other common names for the typical variety include Rocky Mountain redcedar, redcedar, western redcedar, river juniper, cedro rojo, and sabino *(23,42,49)*. Rocky Mountain juniper varies in size from a shrub to a small tree. The largest specimen grows in the Cache National Forest in Utah. It measures 198 cm (78 in) in d.b.h. but is only 11 m (36 ft) tall. Much information is available about Rocky Mountain juniper as a member of a variety of habitat associations; however what is known about the silvics of the species is more limited *(41)*.

Habitat

Native Range

Of 11 junipers native to the United States normally reaching tree size, Rocky Mountain juniper (fig. 1) is the most widely distributed in western North America *(22,49)*. Within its range the distribution is considerably scattered; however, the concentrations, from central British Columbia and southern Alberta through northwestern Montana and southeastern Idaho into Colorado and northern New Mexico, generally follow the Rocky Mountains. In addition, there are fairly extensive concentrations in western portions of the northern Great Plains, in the Uinta and Wasatch Mountains of Utah, and in a band approximately 100 km (62 mi) wide beginning near the Grand Canyon in northwest Arizona and following the Arizona Plateau southeast into the Black Mountains of southwestern New Mexico.

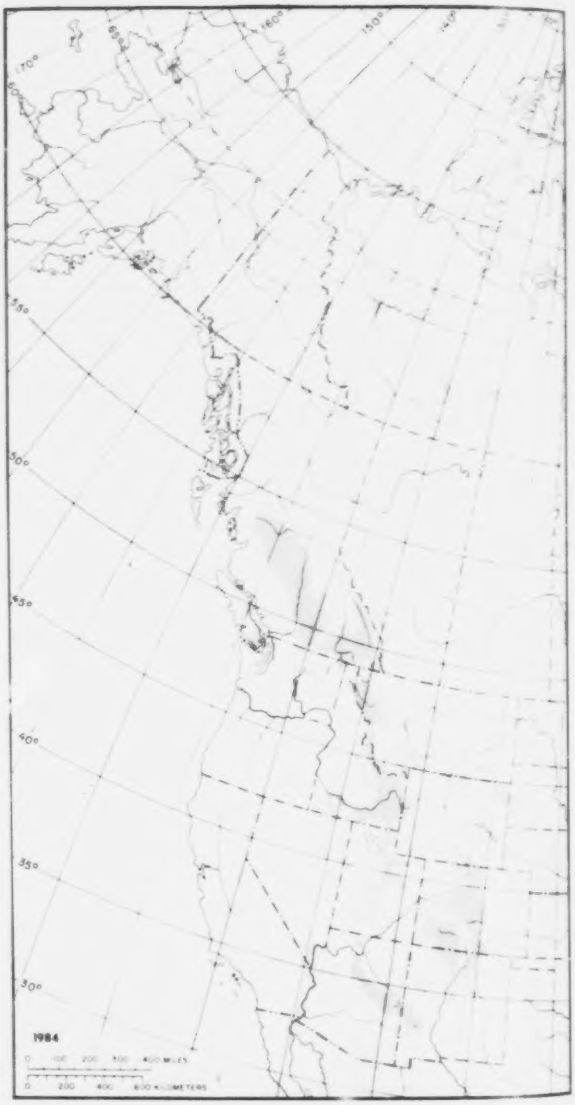

Figure 1—*The native range of Rocky Mountain juniper.*

Climate

The climate generally associated with Rocky Mountain juniper is dry and subhumid. The range of climatic conditions is broad, however, extending from maritime to subalpine to semiarid (table 1). Temperature extremes range from 43° to -37° C (110° to -35° F), but conditions are more favorable to the species when minimum temperatures exceed -23° to -21° C (- 10° to -5° F). Average July temperatures in different areas vary from about 16° to 24° C (60° to 75° F), and average January temperatures from about -9° to 4° C (15° to 40° F). Average number of frost-free days varies from 120 days in parts of the

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Table 1—Climatic data from six regions within the range of Rocky Mountain juniper

Region	Average temperature			Frost-free	Average annual precipitation	
	Annual	July	January	period	Rain	Snowfall
		C		*days*	*mm*	*cm*
Pacific Coast	10	17	3	200+	810	20
Rocky Mountains						
Northern	4	14	−8	120	840	135
Central	7	20	−6	130	330	130
Southern	10	22	−2	150	250	76
Northern Great Plains						
Western area	7	22	−7	140	410	107
Great Basin and						
Southwest	9	21	−1	170	360	147
		F		*days*	*in*	
Pacific Coast	50	63	38	200+	32	8
Rocky Mountains						
Northern	40	58	17	120	33	53
Central	44	68	21	130	13	51
Southern	50	72	28	150	10	30
Northern Great Plains						
Western area	45	72	20	140	16	42
Great Basin and						
Southwest	49	70	30	170	14	58

northern Rocky Mountains to 175 days at lower elevations in Arizona and New Mexico. The longest growing season is near sea level in the Puget Sound area *(36,39,42)*.

Average annual precipitation varies in amount, distribution, and type. Over much of the Rocky Mountain juniper range, precipitation averages 380 to 460 mm (15 to 18 in), with variation from 305 mm (12 in) in areas of the Southwest, Great Basin, and eastern slope of the Rocky Mountains in Colorado to 660 mm (26 in) on Vancouver Island. More than half of the precipitation occurs in late fall or early winter on the Pacific coast and west of the Continental Divide in the northern Rocky Mountains. In the northern Great Plains and east of the divide in the northern and central Rocky Mountains, the period of heaviest precipitation is spring and early summer, but this period is late summer and early fall in the Great Basin, Southwest, and southern Rocky Mountains. In general, snow accounts for about one-third to one-half of the total annual moisture, but the amount is highly variable depending upon location *(44)* (table 1).

Recent paleobotanical studies indicate the macroclimate covering much of the Rocky Mountain juniper range has changed from mesic to more xeric conditions. Rocky Mountain juniper is a drought-enduring species and it is more hardy than eastern redcedar; however it is generally less drought-resistant than other western tree juniper species, and the climatic change has not been favorable for regeneration or growth. Ten-thousand years ago, during the Holocene, the species was present in the Wisconsin forests. As recently as 1,000 years ago, extensive stands of Rocky Mountain juniper were present in Western Nebraska and in the Laramie Basin of Wyoming, with specimens often reaching 131 cm (52 in) d.b.h. *(38,42,45,47)*.

Soils and Topography

Edaphic factors for Rocky Mountain juniper can be characterized as nonspecific and variable, as evidenced by the broad ecological range of the species and its adaptability to a wide variety of soils and conditions in shelterbelt reclamation and landscape plantings. Within pinyon–juniper woodlands in Arizona and New Mexico there are 5 soil orders, 10 great-groups, 40 subgroups, and 150 soil families *(3,16,25,34)*.

Rocky Mountain juniper is most often associated with soils derived from basalt, limestone, and shale throughout its natural range, particularly in semiarid regions. Soils in the order Mollisols are commonly associated with this species. Generally, the soils are poorly developed, stony, shallow, have low moisture-holding capacities and are easily eroded, so that in many places little or no topsoil is present. Some of the soils are calcareous or adobic, often high in clays; are slightly alkaline; and have limy, cemented subsoils. The pH of these soils is generally around 8.0 and moisture availability to plants is low *(21,43)*.

Geology and physiography associated with Rocky Mountain juniper are varied. Throughout its range, it is often found on open exposed bluffs, rocky points, and southern exposures. It does best in sheltered areas, however, along ravines, and in canyons and draws. Its range extends from glaciated valleys in central British Columbia through the foothills of the Rocky Mountains to mesas and tablelands of the southwestern United States, and south into the Sierra Madre in Sonora, Mexico. It is found on lava beds in Idaho and eastern Washington, on limestone cliffs in southwestern Montana, on outcroppings of sandstone and limestone in the central Rocky Mountains, and on high limestone plateaus in South Dakota and Wyoming. It is common on northern aspects in the "badland" topography of both North and South Dakota. In the southern parts of its range, Rocky Mountain juniper is often found on malpais derived from lava flows, and on Kaibab limestone plateaus in northern Arizona *(42)*.

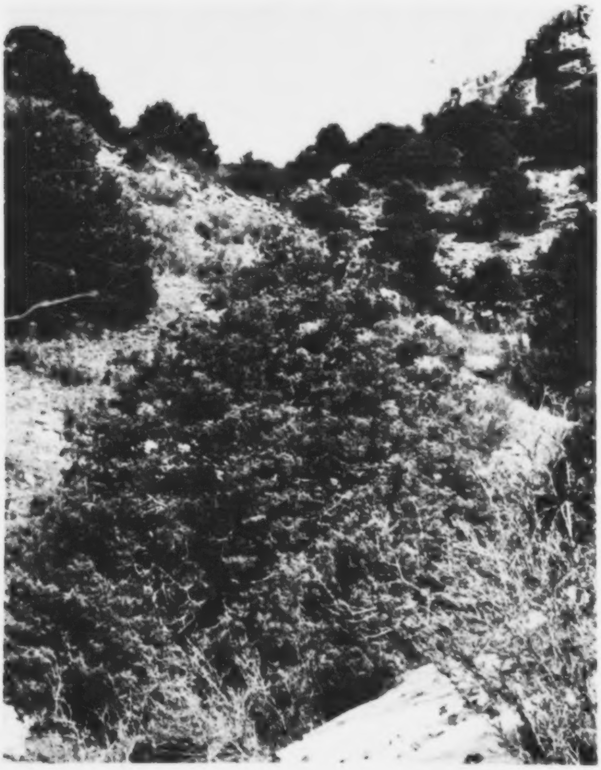

Figure 2—*Pinyon–Juniper (Type 239) near Fort Collins, CO. This is the northern limit for this forest cover type.*

The elevational range of Rocky Mountain juniper is from near sea level to 2740 m (9,000 ft); following the general plant geography rule of decreasing elevation with increasing latitude, the range varies considerably with latitude and local climate. Aspect also has an effect on local elevations, southern exposures generally having a wider range than corresponding northern exposures. For example, in Utah and Nevada, Rocky Mountain juniper has been reported ranging generally from 1070 to 2260 m (3,500 to 7,400 ft) on southern exposures and from 1160 to 1400 m (3,800 to 4,600 ft) on northern exposures *(14,42)*.

Associated Forest Cover

Rocky Mountain juniper is most common as a component of the foothills or woodland coniferous zone; in some areas it extends into the montane zone in significant amounts. It forms a distinct forest cover type, Rocky Mountain Juniper (Society of American Foresters Type 220), from northern Colorado and Utah northward. Southward it becomes associated with Pinyon–Juniper (Type 239) (fig. 2) *(27,36)*.

Rocky Mountain juniper, because of its scattered distribution over a broad range, is often found in complex transition zones or growing on exposed or severe sites within other forest types *(27,36)*. In these situations, however, it is rarely more than a minor component of the forest association. Rocky Mountain juniper is found in the following forest cover types, among others:

206	Engelmann Spruce–Subalpine Fir
208	Whitebark Pine
209	Bristlecone Pine
210	Interior Douglas-Fir
212	Western Larch
216	Blue Spruce
217	Aspen
218	Lodgepole Pine
219	Limber Pine
221	Red Alder
233	Oregon White Oak
235	Cottonwood–Willow
236	Bur Oak
237	Interior Ponderosa Pine
240	Arizona Cypress
241	Western Live Oak

Differences in elevation, latitude, physiography, and soils, which affect temperature, precipitation, soil moisture, and nutrient conditions, in combination with phytozoological interactions, influence the composition of forests in which Rocky Mountain juniper grows. Furthermore, fire has influenced the development of regional differences for Rocky Mountain juniper distribution, associated complexes, and related biotic associations. Only in the northern parts of its range, at middle and lower elevations, does it form pure stands *(14,21,48)*.

Throughout its range south to northern New Mexico and Arizona, Rocky Mountain juniper intermingles with ponderosa pine *(Pinus ponderosa)* on southern and western exposures and with interior Douglas-fir *(Pseudotsuga menziesii* var. *glauca)* on northern and eastern exposures where it is more abundant. At higher elevations, Rocky Mountain juniper is occasionally associated with Engelmann spruce *(Picea engelmannii)*, subalpine fir *(Abies lasiocarpa)*, lodgepole pine *(Pinus contorta)*, and limber pine *(P. flexilis)* throughout the Rocky Mountains. In its central and southern range, Rocky Mountain juniper has been reported with white fir *(Abies concolor)*, blue spruce *(Picea pungens)*, aspen *(Populus tremuloides)*, and narrowleaf cottonwood *(Populus angustifolia)*; at higher elevations it is occasionally or rarely found with bristlecone pine *(Pinus aristata) (36,42)*.

At higher elevations, in British Columbia, Alberta, Idaho, and western Montana, Rocky Mountain juniper is occasionally found with subalpine larch *(Larix lyallii)*, western white pine *(Pinus monticola)*, limber pine, or whitebark pine *(P. albicaulis)*. It is associated with whitebark pine at higher elevations in western Wyoming. In the Pacific Northwest, Oregon white oak *(Quercus garryana)* and red alder *(Alnus rubra)* are commonly associated with Rocky Mountain juniper, along with Douglas-fir at slightly higher elevations on Vancouver Island, the San Juan Islands, and the inland area around Puget Sound *(20,36,42)*.

Rocky Mountain juniper grades into variations of the pinyon-juniper complexes at middle to lower elevations, southward from Nevada, Utah, and Colorado. Within these complexes, Rocky Mountain juniper generally decreases in density in relation to pinyon species with an increase in elevation. The usual junipers are Utah juniper *(Juniperus osteosperma)*, one-seed juniper *(J. monosperma)*, and alligator juniper *(J. deppeana)*. The pinyons may be pinyon *(Pinus edulis)*, Mexican pinyon *(P. cembroides)*, or singleleaf pinyon *(P. monophylla)*. This association is well developed on the Coconino Plateau in Arizona, where it is referred to as the pygmy conifer biome *(14,26,29)*.

Rocky Mountain juniper is often associated with open-grown scrubby ponderosa pine or bur oak *(Quercus macrocarpa)* growing on severe sites in the rough, broken tableland topography of western North and South Dakota and eastern Montana and Wyoming *(27)*. Occasionally in this area, it forms small but almost pure stands (fig. 2). Along stream bottoms and in protected draws, it is occasionally found with a variable but generally incomplete mixture of deciduous trees that may include cottonwood *(Populus* spp.), willow *(Salix* spp.), green ash *(Fraxinus pennsylvanica)*, American elm *(Ulmus americana)*, boxelder *(Acer negundo)*, bur oak, and hackberry *(Celtis occidentalis)*. In the Black Hills, it may, rarely, be found with white spruce *(Picea glauca)*.

Because of Rocky Mountain juniper's association with a wide range of forest-shrub-grassland types, a complete list of understory vegetation would be too long to include here. Sparse understories are a characteristic of Rocky Mountain juniper stands, however, particularly on dry sites and where the species is dominant or codominant. Some of the shrubs reported as understory components are American plum *(Prunus americana)*, antelope bitterbrush *(Purshia tridentata)*, chokecherry *(Prunus virginiana)*, creosotebush *(Larrea tridentata)*, cliffbush *(Jamesia americana)*, cliffrose *(Cowania mexicana)*, red-osier dogwood *(Cornus stolonifera)*, fernbush *(Chamaebatiaria millefolium)*, mountain-mahogany *(Cercocarpus* spp.), rabbitbrush *(Chrysothamnus* spp.), currant *(Ribes* spp.), rose *(Rosa* spp.), sagebrush *(Artemisia* spp.), serviceberry *(Amelanchier* spp.), skunkbush sumac *(Rhus trilobata)*, snowberry *(Symphoricarpos* spp.), winterfat *(Eurotia lanata)*, and shadscale saltbush *(Atriplex confertifolia)*. Also, it shares sites with common juniper *(Juniperus communis)* throughout its range and with creeping juniper *(J. horizontalis)* in the Dakotas, Wyoming, Montana, and Alberta *(20)*.

Common grass and grasslike associates of Rocky Mountain juniper at lower elevations in its northern range include wheatgrass *(Agropyron* spp.), fescue *(Festuca* spp.), needlegrass *(Stipa* spp.), grama *(Bouteloua* spp.), and bluegrass *(Poa* spp.). In the southern Rocky Mountains, it is found with grama, galleta *(Hilaria* spp.), and tobosa *(Hilaria mutica)*. Along its eastern distribution from North Dakota to Texas, Rocky Mountain juniper grows with wheatgrass, grama, buffalograss *(Buchloe dactyloides)*, bluestem *(Andropogon* spp.), and sandreed *(Calamovilfa* spp.) *(20,26)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Rocky Mountain juniper is dioecious. Both pistillate and staminate flowers are small and are borne on the ends of short branchlets or along the branchlet from mid-April to mid-June. The greenish-yellow female flowers usually contain one or two ovules and become more conspicuous during late summer, opening the following spring before pollination. Pollen is disseminated primarily by wind from inconspicuous yellow male flowers on short branchlets, each flower usually containing six stamens. Female flowers are composed of three to eight pointed scales which become fleshy and fuse to form small indehiscent strobili, commonly called "berries" *(15,18)*.

The berries ripen the second year after pollination from mid-September to mid-December and remain on the tree until March or April of the following spring; however, some fruits may persist on the tree for as long as 3 years *(18)*. Immature berries are green and glaucous; ripe berries are bluish purple and covered with a conspicuous white, waxy bloom. The rounded fruit is resinous with a thin coat and averages about 5 to 8 mm (0.2 to 0.3 in) in diameter.

Seed Production and Dissemination—Rocky Mountain juniper may begin bearing seed at 10 years of age, under favorable conditions. The optimum age for seed production is 50 to 200 years. Trees that are open grown, stunted, or under stress often are prolific seed producers. Rocky Mountain juniper is rated as a good to prolific seed producer throughout most of its range, but in parts of Idaho and Montana, production is reported as only fair. The interval between heavy seed crops varies from 2 to 5 years, but some seed is produced almost every year. Rocky Mountain juniper is as good a seed producer as its other tree associates, with the possible exception of Utah juniper and singleleaf pinyon. It is a better producer than common or creeping juniper *(18,42)*.

Each Rocky Mountain juniper fruit usually contains one, sometimes two, and rarely three brownish seeds, and 100 kg (220 lb) of berries yields 11 to 28 kg (24 to 62 lb) of seeds. The angular, lightly grooved seeds are about 5 mm (0.2 in) in length and 3 mm (0.1 in) in thickness; they average about 59 700/kg (27,100/lb) but range from 39 200 to 92 800/kg (17,800 to 42,100/lb) *(18)*.

Rocky Mountain juniper is considered to have a high proportion of unfilled seeds, but the number varies widely from tree to tree and from season to season. Interacting factors causing filled or unfilled seeds are only partially understood; some of the most important are stand age, structure, density, and species composition; physiography; and favorable or unfavorable weather conditions for flower development, pollination, and seed development *(8,18)*.

Viability of Rocky Mountain juniper seed is only fair and, except for alligator juniper, is not as good as other juniper or pinyon species with which it grows. Recent studies indicate that average germinative capacity is 22 percent, with maximums rarely exceeding 35 percent; however, in one study germination averaged 45 percent and varied from 32 to 58 percent. In another study, seed stored in less than ideal conditions had 30 percent germination after 3.5 years. Under proper storage conditions, at least some of the seed may remain viable for several years *(14,18)*.

Rocky Mountain juniper seeds are disseminated primarily by birds, secondarily by gravity and water. A few mammals play a minor role. The berries are eaten mostly during fall and winter months, when other foods are relatively scarce. Bohemian waxwings are known to eat large numbers of berries. Cedar waxwings, robins, turkeys, and the jays—Mexican, pinyon, scrub, Stellar's, and blue—have all been known to feed on the berries at times. As domestic sheep feed on juniper berries, propagation is noticeable along trails between grazing ranges *(30)*. Bighorn sheep and deer occasionally eat the berries, but they normally browse juniper only under stress conditions. Dissemination of seeds by small mammals is thought to be insignificant *(30,33,42)*.

Thus, natural distribution patterns are affected by bird and animal populations, their daily and migratory movements, location and prevalence of berries, and availability and desirability of other foods. These variables, combined with specific site and weather conditions for germination and establishment, are largely responsible for the scattered distribution of Rocky Mountain juniper within its total range.

Artificial regeneration of Rocky Mountain juniper is commercially significant, and large amounts of seed are required to produce the nursery stock needed for planting in shelterbelts, parks, and landscapes, and on mine spoils or other disturbed sites. Fruits should be collected early enough in the fall to avoid losses to birds and animals, but immature fruits should not be gathered because they are difficult to separate from mature fruits *(18)*. Seeds may be stored either in the dried fruits or as cleaned seeds. A moisture content of 10 to 12 percent is considered satisfactory for long-term storage, and the clean seeds or dried fruits should be stored in sealed containers at –7° to 4° C (20° to 40°F).

Normally, Rocky Mountain juniper seeds germinate the second spring after a 14- to 16-month "after-ripening" period that breaks embryo dormancy. Low germination percentages and slow germination, with germination sometimes being delayed more than 2 years, are not unusual, however. These problems result from a combination of chemical factors in the embryo and physical factors, such as the thick, hard, outer layer of the two-layered seedcoat.

which has only a very small permeable area in the hilum *(1,6)*.

Specific effects of passage through the digestive tract of a bird or animal on germination of Rocky Mountain juniper are not known; however, it could improve germination, as digestion acts as a scarification and acid treatment. A report on the pinyon—juniper type states that germination of juniper (species not indicated) was materially improved by such passage *(30)*. Germination is epigeal *(18)*.

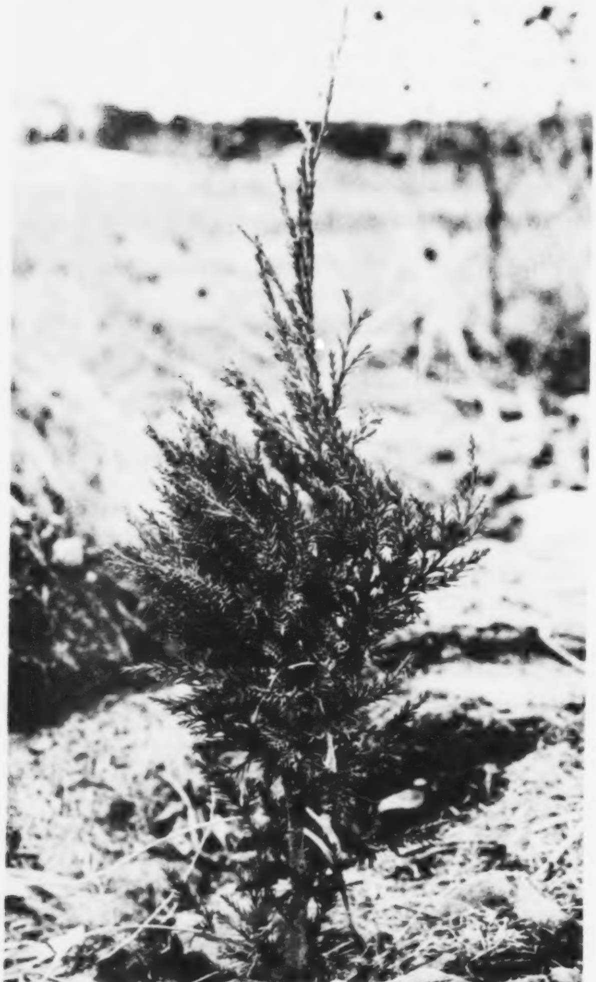

Figure 3—*Three-year-old seedling, 30 cm (12 in) tall, showing immature, acicular foliage. This seedling was outplanted from 2–0 containerized stock. Under natural conditions, at least 8 years of growth are needed to reach this size.*

Seedling Development—Under natural conditions, Rocky Mountain juniper seedlings become established more readily on moist sites under partial shade; in fact, the characteristic sparseness of Rocky Mountain juniper regeneration is due partly to its inability to establish itself on drier sites. The moist sites favored by Rocky Mountain juniper often are conducive to frost-heaving, however, which can take a heavy toll of seedlings. In nurseries, seedlings are best established on mulched seedbeds under partial shade *(2,18,42)*.

The seedlings, characterized by acicular foliage (sharp-pointed leaves) (fig. 3), develop slowly under natural conditions. They are reported to reach a height of 30 cm (12 in) in 8 years in northern New Mexico and Arizona. Their growth is more rapid in nurseries, where they often reach 15 cm (6 in) or more in 3 years. The preferred age for nursery stock for field plantings depends on the area and includes 2–0, 3–0, 1–1, 1–2, 2–1, or 2–2 stock. Potting or

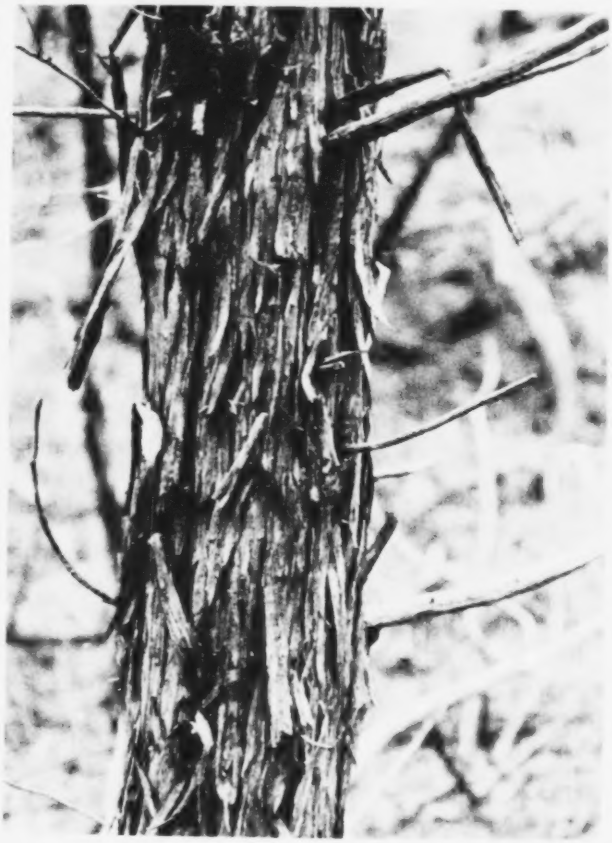

Figure 4—*Fibrous, stringy bark, characteristic of mature Rocky Mountain juniper.*

balling Rocky Mountain juniper for field planting increases survival over bare root planting during dry years but adds considerably to the cost. During the fall, seedlings often change from the normal green to a bluish purple because of freezing weather, less precipitation, or changes in light intensity *(18,42)*.

Seedlings in the juvenile stages are sometimes confused with common juniper seedlings, but they do not have the basally jointed leaves of that species *(15)*.

Vegetative Reproduction—Rocky Mountain juniper does not reproduce naturally by sprouts or layering. Cuttings can be grown satisfactorily in a rooting medium if they are given a basal treatment of indolebutyric acid in talc and misted intermittently for 3 s/min *(12,42)*.

Sapling and Pole Stages to Maturity

In the sapling stage, Rocky Mountain juniper has mature foliage characterized by small, somewhat obtuse, scalelike leaves. The sapling bark is usually reddish brown and slightly rough and scaly, but not stringy and fibrous as when mature (fig. 4) *(14,15)*.

Mature Rocky Mountain juniper can vary from shrub size to small trees, with wide variation in crowns. Typically, it has a central trunk and a conical crown, slightly more rounded than eastern redcedar with which it is often confused *(37)*. Branches are spreading, normally extending to ground level; small branches often droop slightly. Mature trees, as well as saplings, vary in color from light green or a yellowish green to dark green. The presence of mature fruits can give the tree a bluish-green or gray appearance.

Growth and Yield—Rocky Mountain juniper grows slowly and rather uniformly throughout its range; however, rates of growth have not been thoroughly studied. In the Southwest, average height at 40 years of age has been reported to be about 4 m (13 ft), indicating a growth rate of 10.3 cm (4.1 in) per year. At age 40, height growth declines to about 3.4 cm per year (1.3 in) until age 80, at which time trees average about 5 m (18 ft) tall. Thereafter, height growth is fairly uniform at 1.8 cm per year (0.7 in), producing trees 9 m (30 ft) tall at about 300 years of age. Diameter growth measured at 30 cm (12 in) above the ground (basal diameter) was also reported as slow, with a growth rate of 0.2 cm (0.08 in) per year. This growth rate is fairly uniform until the trees are about 170 years old or average about 33 cm (13 in) in basal diameter. The rate then declines over a period of about 40 years to another constant rate of about 0.08 cm (0.03 in) per year when the tree is 210 years old. This growth rate may be sustained until the tree is 300 or more years old. Basal diameters of trees 300 years old averaged 43 cm (17 in). The species is long lived, with ages of 300 years not uncommon. A relic specimen in western South Dakota was estimated to have been 750 years old when it died; one unusual specimen in Logan Canyon, UT, is reported to be 3,000 years old *(4,42)*.

Tree growth varies considerably with location and site condition. In Canada, the trees usually grow to 30 cm (12 in) in basal diameter and 3 to 4 m (10 to 12 ft) tall, although a few trees reach 9 m (30 ft) in height. Trees on the north rim of the Grand Canyon are 5 to 6 m (15 to 20 ft) tall and 30 to 46 cm (12 to 18 in) in basal diameter. Heights of 6 to 15 m (20 to 50 ft) and basal diameters up to 46 cm (18 in) are reported from other areas of the Southwest *(14,42)*.

Rocky Mountain juniper is not recognized as a commercial timber species, so limited volume and growth prediction data are available. Stand yield prediction equations have been developed for the species in Colorado, Idaho, Utah, and Wyoming. Most information available is generalized and related to harvesting for fenceposts and firewood and to management of stands for watershed, range, wildlife and shelterbelts. It is a fragile forest type and overcutting or improper management for livestock use reduces wildlife habitat and damages watershed *(5,30)*.

The future management of Rocky Mountain juniper as a forest type, of which only about 22 percent is in national forests, is unclear; furthermore, present conditions for management are not well known. As an associate of the pinyon–juniper type, the species is recommended for 200-year-rotation management and both even- and uneven-aged silvicultural systems can be applied. In the past, harvesting varied from light-cutting and high-grading to excessive overcutting; in recent years pinyon–juniper has been removed from large areas by chaining to increase forage for livestock. Except in limited areas in rather inaccessible places, few so-called virgin stands remain *(1,10,30)*.

Rooting Habit—Rocky Mountain juniper is considered to have a shallow but fairly extensive lateral root system, particularly where trees are growing over cemented subsoils or in rocky areas that limit depth of root penetration. The species develops a deeper root system along bottom lands with deeper soils. In the nursery, undercutting of third-year seedlings stimulates strong lateral root development *(18)*.

Reaction to Competition—Rocky Mountain juniper normally is a component of long-term seral or near-climax vegetation. It is relatively shade-tolerant during the seedling and sapling stages, but it later becomes more intolerant and is unable to endure as much shade as eastern redcedar—its eastern counterpart. Rocky Mountain juniper requires top light for height growth and crown development, and trunk branches die out when it develops in overly dense, pure stands or under deep shade of other tree species. In the northern Rocky Mountains, it is considered less tolerant of shade than ponderosa pine, limber pine, or lodgepole pine but is reported to endure considerable shade from broadleaf trees in protected canyons and sheltered sites on the Pacific coast *(26,42)*. Overall, it is most accurately classed as a very shade-intolerant species.

In Utah, junipers have been observed to invade sagebrush stands under certain conditions; pinyon generally follows and has a tendency to replace the juniper. Pinyon–juniper may encroach into grasslands that have been overused or disturbed in some manner, as juniper germination and establishment are favored by mineral soil. Rocky Mountain juniper also has allelopathic properties that can inhibit establishment of competing grasses, forbs, and shrubs. Herbicides can be used to kill individual trees, to keep chained areas from revegetating, and to restore recently invaded grasslands. However, Rocky Mountain juniper and one-seed juniper are the most difficult of the juniper species to kill *(17,24,26,28,42)*.

Controlled burning to reduce competition from juniper species has had varied results. Insufficient ground-fuel and wide topographical and meteorological variables make it difficult to use fire throughout the entire range of Rocky Mountain juniper. Generally, fire has been more successful in the southern areas of the species' range *(48)*.

Once established, Rocky Mountain juniper competes well with understory vegetation for water and minerals. In a shelterbelt study, its height growth exceeded Siberian pea shrub, green ash, boxelder, or American elm when competing with undisturbed sod-forming grasses. Removal of the sod did increase juniper growth, but not significantly *(34)*.

Apparently no silvicultural guidelines or cutting methods have been developed for Rocky Mountain juniper. Its shade tolerance when young would tend to rule out the clearcut method. Development of shade intolerance with maturity might suggest a three- or four-step shelterwood system, should a need develop to grow and harvest Rocky Mountain juniper in pure stands.

Damaging Agents—Rocky Mountain juniper is susceptible to loss from erosion simply because it often becomes established on exposed sites where soils are readily eroded. Overuse of ranges by livestock, bison (in North and South Dakota), and occasionally deer can accelerate the erosion process.

Because animals use the trees as "rubbing posts," they cause considerable physical damage to stems and roots, including wounds that may admit pathogens. In addition, they browse the foliage when range conditions are poor and animal concentrations are high. This browsing, called "high-lining," reduces crown size, ultimately affecting growth and vigor.

Rocky Mountain juniper is attacked by a complex of arachnids, insects, and nematodes *(11,37)*. Two species of spider mites *(Oligonychus ununguis* and *Eurytetranychus admes)* feed on foliage and occasionally develop epidemic populations. Two species of juniper berry mites *(Trisetacus quadrisetus* and *T. neoquadrisetus)* that destroy the fruits have been reported in British Columbia and Oregon *(35)*. A small red false spider mite *(Pentamerismus erythreus)*, sometimes called red spider, is not rated as a forest pest but can be a serious problem in shelterbelts and landscape plantings.

Rocky Mountain juniper is host to several species of Coleoptera (true insects), Lepidoptera (butterflies and moths), Diptera (flies and midges), and Psyllids (jumping plant lice) that damage the roots, bole, twigs, foliage, and berries.

A nematode, *Pratylenchus penetrans*, has injured Rocky Mountain juniper seedlings by causing root lesions. The damage has been reported only in the nursery, where populations of the nematode have reached high levels *(13)*.

A broad range of diseases associated with Rocky Mountain juniper attack the roots, stems, and foliage; but the most serious disease probably is a blight caused by *Cercospora sequoiae*. Some shelterbelts in the Great Plains have lost most of their junipers from this disease. Rocky Mountain juniper is also an alternate host for a cedar-apple rust *(Gymnosporangium juniperi-virginianae)* which can be a serious problem in the apple industry. The most conspicuous stem diseases are rusts caused by *Gymnosporangium* spp. and by mistletoes *(Phoradendron* spp.). These infestations generally are noted by the formation of twig excrescences, woody galls, and witches' brooms *(13,19)*.

Seedling diseases of Rocky Mountain juniper have not been thoroughly studied. It is normally resistant to damping-off fungi; however, *Rhizoctonia solani* has caused losses in Texas *(12)*. Phomopsis blight *(Phomopsis juniperovora)* can destroy seedlings in the nursery and reduce survival of outplanted seedlings from partial blighting of the foliage. This blight is seldom found on trees older than 4 years; the disease does not thrive under the dry conditions prevailing on most juniper sites. In some nurseries, juniper cultivars have developed magnesium-deficiency symptoms that were similar to symptoms of Phomopsis blight.

Ectotrophic mycorrhizae are rare on the Cupressaceae. Most *Juniperus* species examined have been primarily endomycorrhized. No fungi have been reported to form mycorrhizae with Rocky Mountain juniper. *Tuber griseum* and *T. melanosporum* have been reported with juniper species in general, however, and *Elaphomyces granulatus* had been reported for common juniper *(13,40)*.

Rocky Mountain juniper is susceptible to death or severe injury from fire, primarily because the fibrous, stringy bark is thin, and the lower branches contain significant amounts of volatile oils and normally extend to the ground *(13)*.

Special Uses

The early Indians made some use of juniper berries for food and decoration; the bark was woven into cradles and similar products as well as being used for torches. The most important use of Rocky Mountain juniper, however, was as firewood for cooking and heating, and today this is still a major use. Fuelwood volume tables that include Rocky Mountain juniper have been developed *(14,30)*.

The wood is fine grained, with white sapwood and deep red heartwood with faint purplish and whitish streaks. It is slightly lighter in weight and not as hard as that of eastern redcedar, but in color, odor, figure, and strength it could be substituted for its eastern counterpart. When cured, the wood, especially the heartwood, is resistant to decay; it has been cut heavily for fenceposts, particularly before the advent of steel fenceposts *(14)*.

The small size and rapid taper of the stems, with the consequent high cost of producing usable sawn material, have discouraged use for lumber. However, some sawn material has been cut from Rocky Mountain juniper for such use as closet lining, custom-built furniture, inlays, and cedar chests. The products are attractive; the colored heartwood also has been used for carvings and novelties, but only on a small scale *(14,30)*.

Genetics

Population Differences

Information on population variability of Rocky Mountain juniper is incomplete. Undoubtedly, any species with its scattered distribution and wide elevational and latitudinal range will show differences between subsets of the total population in such features as growth, morphology, phenology, and resistance to heat and cold. Recent studies on variations of terpenoids, other volatile oils, and isozymes are providing more information about differences not only among individuals but among segments of the population *(31)*. A study on the overlapping populations of Rocky Mountain juniper and eastern red cedar in the Missouri River Basin indicates that secondary intergradation (allopatric introgression) is occurring rather than primary intergradation (allopatric divergence), and the gene flow is primarily in an easterly direction *(9)*.

Races and Hybrids

Hybridization and the development of races of Rocky Mountain juniper are complex. The whole population within the Missouri River Basin is reported to be a hybrid swarm of Rocky Mountain juniper and eastern redcedar, with neither of the extreme parental types being found; also, the trees tend increasingly toward Rocky Mountain juniper in a line from the southeast to the northwest. It has been shown that controlled hybridization between these two species is possible. A triparental hybrid swarm that includes horizontal juniper and eastern redcedar *(J. virginiana)* has also been reported in western portions of the northern Great Plains. In the Southwest, hybridization with alligator juniper has been reported *(7,8,14,46)*.

No subspecies have been identified for Rocky Mountain juniper. Two naturally occurring varieties have been reported. *J. scopulorum* var. *columnaris*, a columnar form, is found only in North Dakota. A depressed shrub, *J. s.* var. *patens*, found in Wyoming and Alberta, is considered to be a hybrid with horizontal juniper *(32,42)*.

Several horticultural and ornamental varieties have been reported. Most of these have been developed from the natural columnar variety in North Dakota and from the ornamental variety *J. scopulorum* var. *viridifolia*, called "Chandler Blue" and "Hill Silver" *(16)*. Other varieties include "Medora," a bluish, semicolumnar compact form; "Moffet," similar to Medora but somewhat less compact; "Welch," a blue-green pyramidal type with upright branches; "Pathfinder," a silver-blue type of more open form; "Colorgreen," a reasonably compact green variety; and "Hillborn Globe," a broad, blue-green pyramid form. Most of these varieties have been introduced into the horticultural trade as grafted specimens.

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Juniperus silicicola (Small) Bailey Southern Redcedar

Cupressaceae Cypress family

L. P. Wilhite

Southern redcedar (*Juniperus silicicola*), also called redcedar, coast juniper, sand-cedar, and eastern redcedar, has not been well studied. Until more work is done, the fragmentary information available should be supplemented, though cautiously, with information in the literature about eastern redcedar (*J. virginiana*). The two species are similar in many respects. Generally, eastern redcedar has ascending or horizontal branches, male cones 3 to 4 mm (0.12 to 0.16 in) long, and female cones 5 to 6 mm (0.20 to 0.24 in) long containing one to four seeds. In contrast southern redcedar generally has more slender, pendulous branches, male cones 5 to 6 mm (0.20 to 0.24 in) long, and female cones 3 to 4 mm (0.12 to 0.16 in) long containing only one or two seeds (*5,11*).

Habitat

Native Range

The native range of southern redcedar (fig.1) extends from coastal North Carolina through northern Florida and across the Gulf Coast to eastern Texas. Except in the center of the Florida peninsula and in outliers in Louisiana and Texas, the species is found within 50 km (30 mi) of saltwater.

On the range map, the inland boundary of the species should not be considered exact because it touches or overlaps the southern boundary of eastern redcedar, which so resembles southern redcedar that the two often are confused.

Climate

Two climatic types, humid and moist subhumid, are present within the range of southern redcedar. Normal precipitation increases from about 1200 mm (48 in) per year in the Carolinas to more than 1600 mm (63 in) along the central Gulf Coast, then decreases to about 1000 mm (40 in) in eastern Texas. Length of growing season varies from about 240 days in North Carolina, Louisiana, and Texas to more than 330 days along both coasts of central peninsular Florida. Southern redcedar is found from slightly north to slightly south of U.S. Department of Agriculture Plant Hardiness Zone 9, which is defined by a range in average minimum temperatures from -7° to -1° C (20° to 30° F).

Soils and Topography

Southern redcedar is mostly restricted to the nearly flat outer Coastal Plain, so its establishment and growth in relation to topographic factors are not well understood.

Along the Atlantic and Gulf Coasts, southern redcedar is associated with limestone outcroppings and Indian shell middens bordering tidal marshes, and on sea islands on the leeward side of dunes, where salt spray is minimal. On the Gulf Coast, the species often is found in a narrow zone between the tidal marsh and the pine flatwoods (*7*). Also along the Gulf Coast, it often colonizes dredge spoil islands (*3*).

Inland from the coast, scattered individuals of the species can be found from the broad, flat ridges between streams to the flood plains of these streams. In areas of abandoned rice fields in South Carolina, the species is found more frequently on the tops and sides of the old dikes than in the poorly drained flats between them.

The natural range of southern redcedar includes soils belonging to the orders of Alfisols, Entisols, Inceptisols, Spodosols, and Ultisols (*14*). Redcedars usually are found on soils that are moist or wet, but not saturated. In general, the species appears to prefer sites of high base saturation, as indicated by its presence near sources of limestone or on Alfisols.

Associated Forest Cover

Southern redcedar is the predominant species in the forest cover type Southern Redcedar (Society of American Foresters Type 73), in which it occupies a plurality (20 to 50 percent) of the basal area (*4*). Common overstory associates in this type are live oak (*Quercus virginiana*), sand live oak (*Q. virginiana* var. *germinata*), cabbage palmetto (*Sabal palmetto*), slash pine (*Pinus elliottii*), southern magnolia (*Magnolia grandiflora*), laurel oak (*Quercus laurifolia*), redbay (*Persea borbonia*), and American holly (*Ilex opaca*). Common understory species are yaupon (*I. vomitoria*), southern bayberry (*Myrica cerifera*), devilwood (*Osmanthus americanus*), Carolina laurelcherry (*Prunus caroliniana*), beautyberry (*Callicarpa americana*), bumelia (*Bumelia* spp.), tree sparkleberry (*Vaccinium ar-*

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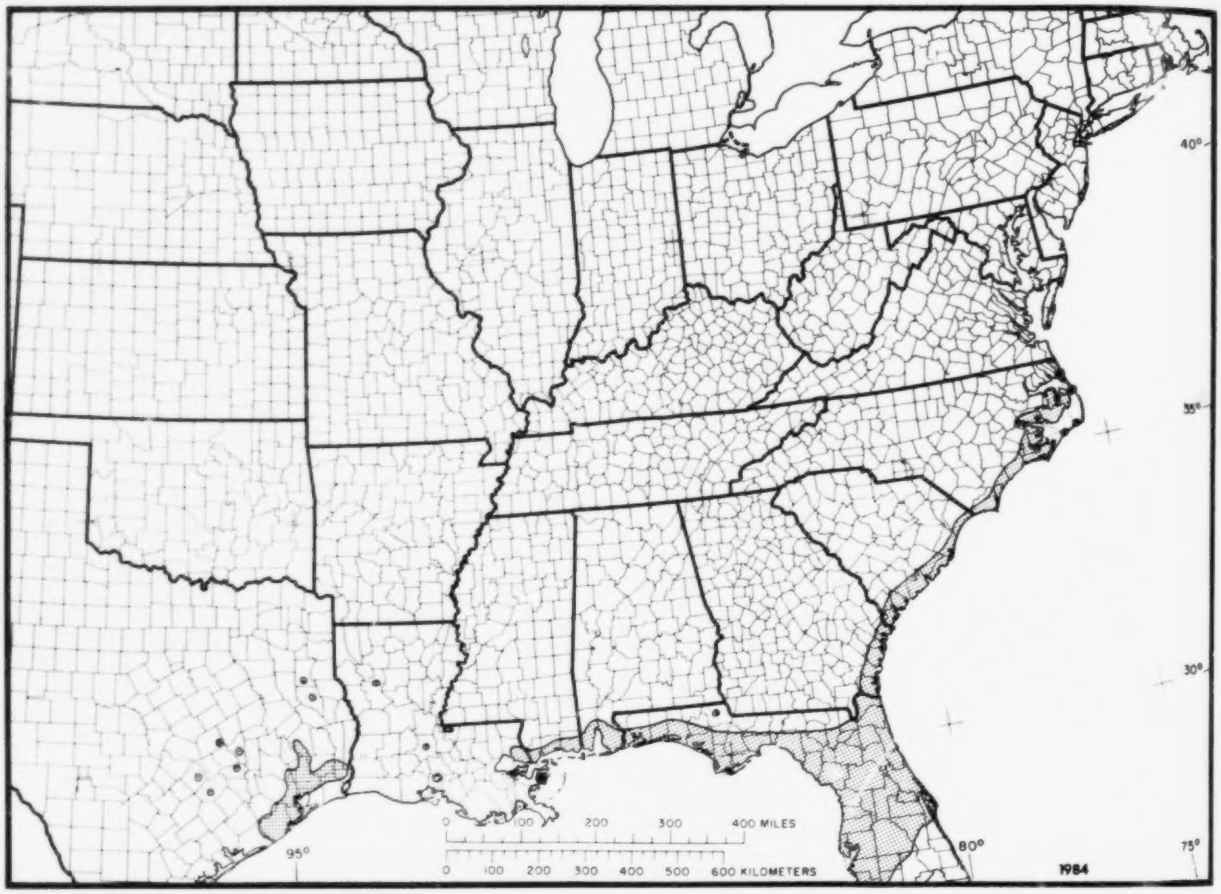

Figure 1—*The native range of southern redcedar.*

boreum), muscadine grape *(Vitis rotundifolia)*, and greenbriers *(Smilax* spp.).

Southern redcedar was virtually eliminated as an overstory species during the 19th century by harvesting, primarily for the manufacture of pencils. Live oaks and other associated trees were not cut at that time, and their competition presumably has retarded the reestablishment of cedar-dominated stands. Consequently, Southern Redcedar (Type 73) is quite similar to Cabbage Palmetto (Type 74). Both of these types are variants of a general maritime forest.

Inland from this maritime forest, the Southern Redcedar type sometimes intergrades with Sweetbay–Swamp Tupelo–Redbay (Type 104). Southern redcedar is listed as a minor species in Slash Pine (Type 84), and it has been found in Loblolly Pine (Type 81). In these pine types, redcedars seldom reach the overstory, possibly because of competition from the pines and associated hardwoods.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Southern redcedar is dioecious. The male cones shed pollen in January to February, and the berrylike female cones, dark blue and covered with a glaucous bloom, mature in October to November of the first year *(11)*. Seeds often have dormant embryos, and germination may not occur until the second or third spring after seed maturation *(2)*. Cold stratification, however, hastens germination, and so might stratification of the seed by passage through the digestive system of an animal. Germination is epigeal. Southern redcedar should be sown in fall or cold-stratified and sown in either fall or spring *(13)*.

Seed Production and Dissemination—There is considerably more information on the reproduction of eastern redcedar than on southern redcedar. Eastern redcedar produces some seeds nearly every year with irregular heavy seed crops. Its seeds are dispersed in the fall, usually by birds. Seeds may be stored as dried fruits or after extraction with a macerator. Cleaned seeds range from 81 600 to 121 300/kg (37,000 to 55,000/lb). A citric acid soak preceding cold stratification increases germination more than cold stratification alone *(13)*.

Seedling Development—Stratified seeds of eastern redcedar sown in the spring should be in the ground early enough to ensure complete germination before air temperatures exceed 21° C (70° F), and complete germination requires 4 to 5 weeks. Juniper seeds are usually drilled into rows 15 to 20 cm (6 to 8 in) apart and covered with about 0.6 cm (0.25 in) of firmed soil. The beds should be mulched with straw, sawdust, burlap, or plastic film, and the mulch removed as soon as germination starts. Light shade should be provided during the first growing season. Eastern redcedar is planted as 2–0, 3–0, 1–1, 1–2, 2–1, or 2–2 stock. Potting or balling for field planting increases survival over bare-root planting during dry years *(13)*.

Vegetative Reproduction—Southern redcedar can be propagated by cuttings of nearly ripened wood *(2)*. The closely related species, eastern redcedar, can be propagated by rooted cuttings, but there is much variability among varieties within the species as to ease of rooting. Rooting success has been increased by treatments with indolebutyric acid, naphthalene acetic acid, and Phygon XL talc. Because of the difficulties and inconsistencies in rooting juniper cuttings, grafting has long been the standard method of propagating clonal material of eastern redcedar *(18)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Little is known about the growth of this species. It has been reported to be moderate in growth rate *(1)* or to be long lived and slow growing *(17)*. Mature height has been reported to be about 8 m (25 ft) *(1,2,19)* or about 15 m (50 ft) *(9,12)*. The largest southern redcedar recorded by the American Forestry Association was 21 m (70 ft) tall and 145 cm (57 in) in d.b.h. in 1976 *(10)*. Some of the virgin timber along Apalachee Bay in Florida may have been more than 30 m (100 ft) tall *(3,4)*. Perhaps the second-growth timber of this long-lived species has not yet reached its mature height on its best sites (fig. 2).

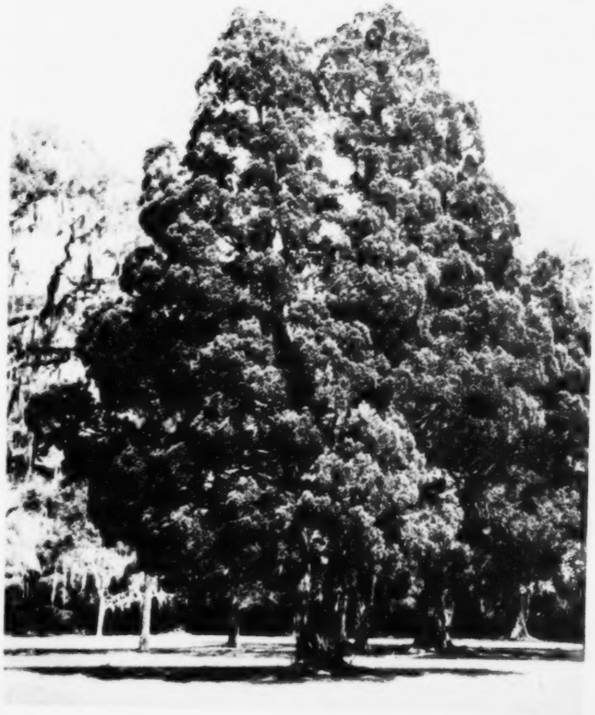

Figure 2—*A mature southern redcedar on Cape Romain Migratory Bird Refuge, SC.*

Rooting Habit—The species has been reported to have a shallow root system *(17)*.

Reaction to Competition—Brief statements in the literature, plus observations, indicate that southern redcedar can become established and will grow in sun or partial shade. Competition, however, may retard reestablishment of cedar-dominated maritime forests because of the dense shade cast by live oaks and associated hardwoods. Southern redcedar, like eastern redcedar, is classed as intolerant to very intolerant of shade. The fact that southern redcedar often grows on the margins of tidal marshes indicates that it is fairly tolerant of salt spray, wind, and flooding *(1,12,17)*.

Damaging Agents—Fire is deleterious to this thin-barked species, but the forest cover type

Southern Redcedar, which is generally found on sea islands or immediately inland from salt marshes of the mainland, rarely experiences fire. Farther inland, where southern redcedar occurs as a minor species and fires are more frequent, it suffers damage and mortality. Fire damage may be less prevalent now than in the past. Control of wildfires has allowed eastern redcedar to come back to sites within its natural range where it has not existed for a long time *(18)*, and conditions are similar for southern redcedar within its natural range.

Cedar-apple rust *(Gymnosporangium juniperi-virginianae)* attacks southern redcedar *(6)*, and bagworms *(Thyridopteryx ephemeraeformis)* have been observed feeding on its foliage. Other agents that damage eastern redcedar, such as cedar blight *(Phomopsis juniperovora)* and various wood rots *(15)*, probably damage southern redcedar also.

Special Uses

Southern redcedar lumber is used in the manufacture of chests, wardrobes, closet linings, flooring, and scientific instruments. Because the heartwood of redcedar is very resistant to decay, it is used for fence posts *(16)*. Young southern redcedars are sold as Christmas trees *(2)*.

Junipers, including southern redcedar, furnish fruit, browse, and protective and nesting cover for many species of wildlife *(8)*.

In landscaping, southern redcedar is used as a background, windbreak, or hedge in parks and along roadsides or around homes *(1,2)*. Although usually found on moist soil, it will grow in dry, sandy, or rocky land, and this hardiness, plus its salt tolerance, makes it desirable for ocean bluffs and seaside plantings.

Genetics

Southern redcedar apparently hybridizes freely with eastern redcedar *(18)*. The literature contains nothing else on the genetics of southern redcedar.

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Juniperus virginiana L. Eastern Redcedar

Cupressaceae Cypress family

Edwin R. Lawson

Eastern redcedar *(Juniperus virginiana)*, also called red juniper or savin, is a common coniferous species growing on a variety of sites throughout the eastern half of the United States. Although eastern

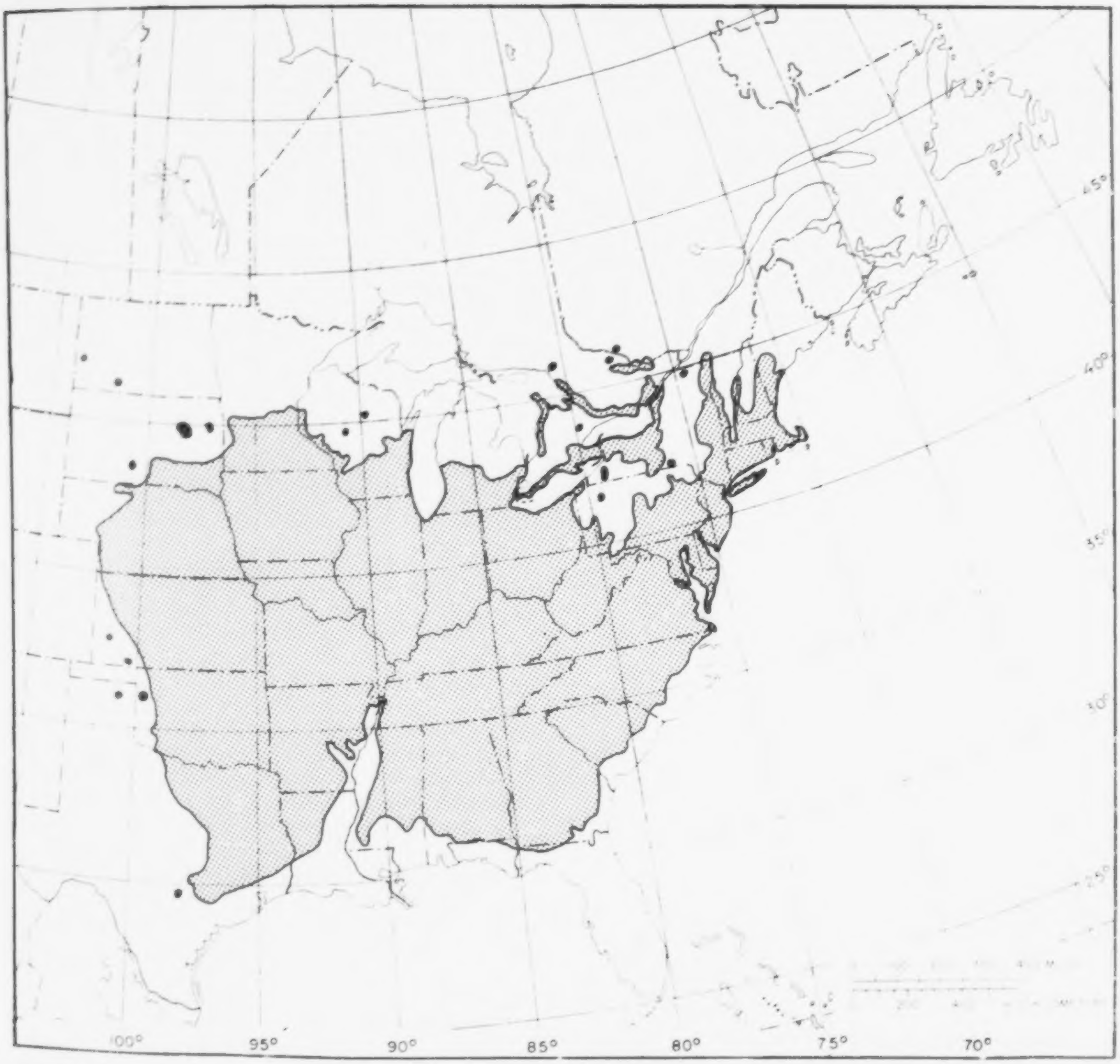

Figure 1—*The native range of eastern redcedar.*

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redcedar is generally not considered to be an important commercial species, its wood is highly valued because of its beauty, durability, and workability. The number of trees and volume of eastern redcedar are increasing throughout most of its range. It provides cedarwood oil for fragrance compounds, food and shelter for wildlife, and protective vegetation for fragile soils.

Habitat

Native Range

Eastern redcedar (fig. 1) is the most widely distributed conifer of tree size in the Eastern United States and is found in every State east of the 100th meridian. The species extends northward into southern Ontario and the southern tip of Quebec *(27)*. The range of eastern redcedar has been considerably extended, especially in the Great Plains, by natural regeneration from planted trees *(47)*.

Climate

The wide natural distribution of eastern redcedar clearly indicates its ability to grow under varying and extreme climatic conditions. Average annual precipitation varies from about 380 mm (15 in) in the northwestern section to 1520 mm (60 in) in the southern parts of its range *(40)*. Throughout the eastern redcedar range, average precipitation from April through September measures from 380 mm (15 in) to 760 mm (30 in). This suggests that summer precipitation may be more limiting to the species than average annual precipitation. Average annual snowfall ranges from a trace to more than 254 cm (100 in).

Table 1—Site classes for natural stands of eastern redcedar in northern Arkansas

	Site class			
Item	**I**	**II**	**III**	**IV**
Soil character	alluvial	upland	upland	upland
Soil depth, cm	61+	61+	30 to 58	less than 30
Soil depth, in	24+	24+	12 to 23	less than 12
Site index[1]				
Open stand, m	16.8	13.7	10.7	7.6
Open stand, ft	55	45	35	25
Closed stand, m	18.3	15.2	12.2	9.1
Closed stand, ft	60	50	40	30

[1] Adjusted to base age 50 years.

Average annual temperatures vary from about 4° C (40° F) in the north to 20° C (68° F) in the southern part of the botanical range. Average annual maximum temperature ranges only from about 32° C (90° F) to 41° C (105° F), but average minimum temperature ranges from −43° C (−45° F) to −7° C (20° F). The growing season varies from about 120 to 250 days.

Soils and Topography

Eastern redcedar grows on a wide variety of soils, ranging from dry rock outcrops to wet swampy land *(15)*. The most common soils fall within the soil orders Mollisols and Ultisols. No attempt will be made here to describe all of them. Like most species, eastern redcedar grows best on deep, moist, well-drained alluvial sites, where its height may reach 17 to 18 m (55 to 60 ft) in 50 years. On the better sites, however, hardwood competition is so severe that the species rarely becomes dominant. Eastern redcedar also grows well on deep, upland soils, particularly abandoned farmland. A 0.4-hectare (1-acre) plantation established in Arkansas from wildlings, with spacing of 1.8 by 1.8 m (6 by 6 ft), yielded a basal area of 37.4 m^2/ha (163 ft^2/acre) and an estimated 196 m^3/ha (2,800 ft^3/acre) of merchantable volume in 44 years *(11)*.

The species is frequently associated with areas commonly called glades, characterized by thin rocky soils and intermittent rock outcrops; soil depth is difficult to determine because soil rock content and depth of rock fissures vary *(11,16)*. Soils on the poorest glade sites are less than 30 cm (12 in) deep, medium sites are usually less than 61 cm (24 in) deep and have large crevices, and good sites have deeper soil. Arend and Collins *(3)* developed the site classification system shown in table 1.

Eastern redcedar grows on soils that vary widely in acidity. Soils found in natural stands range in pH value from 4.7 to 7.8. Although the species will grow on sites that are slightly alkaline, it is not particularly tolerant to higher pH levels. Eastern redcedar is, in fact, among the least alkali-tolerant of drought-hardy trees and shrubs. Soils in eastern redcedar stands tend to become neutral or slightly alkaline because the high calcium content of the tree's foliage can change the pH of the surface soil in a relatively short time. This condition also increases earthworm activity, with an increase in incorporation of organic matter, a lower volume weight, and an increase in pore volume and infiltration rate *(11,15)*.

Eastern redcedar grows on ridgetops, varying slopes, and flat land and is frequently found on dry, exposed sites and abandoned fields. Aspect also in-

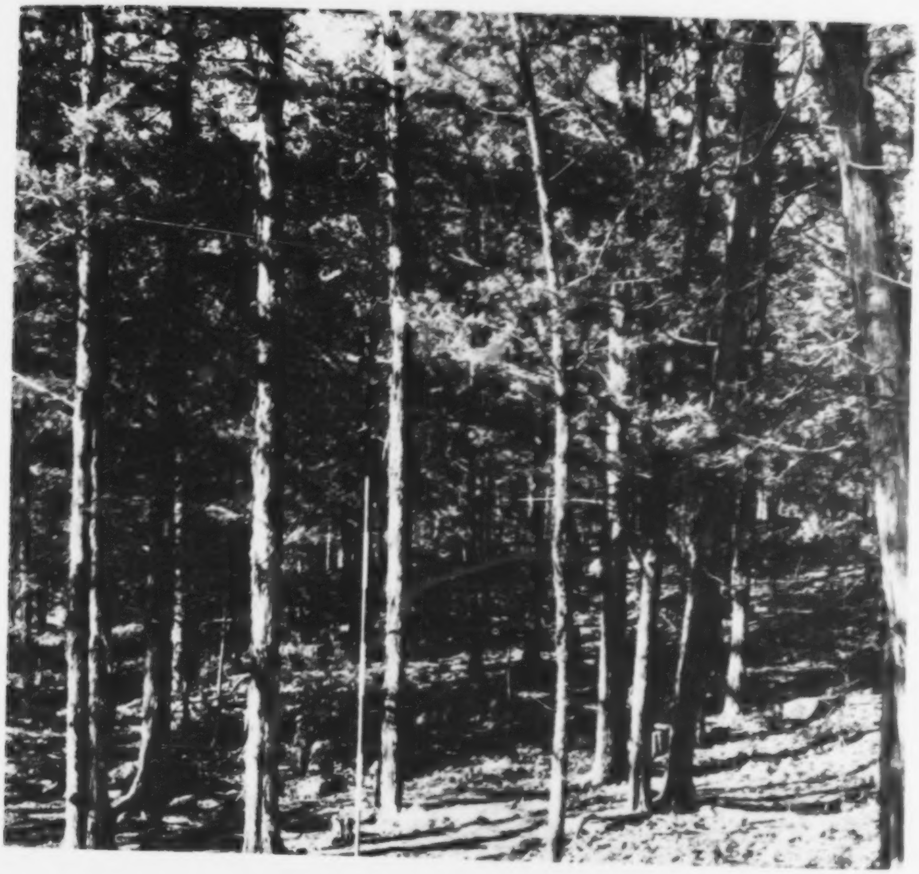

Figure 2—*Nearly pure stand of eastern redcedar on an upland site.*

fluences eastern redcedar development. In the western part of its range, the species may be found on north-facing slopes and along streambanks where there is some protection from high temperatures and drought. Although the most desirable elevation is not clearly delineated, eastern redcedar is found most often growing between 30 m (100 ft) and 1070 m (3,500 ft). It is notably absent below the 30 m (100 ft) elevation zone in the southern and eastern parts of the species range *(15,27)*.

Associated Forest Cover

Pure stands of eastern redcedar are scattered throughout the primary range of the species. Most of these stands are on abandoned farm lands or drier upland sites (fig. 2). The forest cover type Eastern Redcedar (Society of American Foresters Type 46) is widespread and therefore has many associates *(10)*. Variants of the type are eastern redcedar-pine, eastern redcedar-hardwood, and eastern redcedar-pine-hardwood. The eastern redcedar-pine variant is composed of eastern redcedar and either shortleaf pine (*Pinus echinata*) or Virginia pine (*P. virginiana*) and is found throughout the southern half of its range. The eastern redcedar-hardwood variant is found throughout the central part of its range and includes a mixture of red (*Quercus rubra*) and white (*Q. alba*) oaks, hickories (*Carya* spp.), black walnut (*Juglans nigra*), and other hardwoods. The third variant, eastern redcedar-pine-hardwood, includes all of the above species associations *(15)*. Eastern redcedar appears as a minor component of several other forest cover types.

Eastern redcedar is among the first to invade abandoned fields and areas cleared for pasture *(25)*. On deeper soils, persimmon (*Diospyros virginiana*) and sassafras (*Sassafras albidum*) are associated invaders and may crowd it out. In cedar glades, the species is commonly associated with blackjack oak (*Quercus marilandica*), winged elm (*Ulmus alata*), fragrant sumac (*Rhus aromatica*), Carolina buckthorn (*Rhamnus caroliniana*), rusty blackhaw (*Viburnum rufidulum*), and Alabama supplejack (*Berchemia scandens*). Little bluestem (*Andropogon scoparius*), big bluestem (*A. gerardi*), yellow Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), dropseed (*Sporobolus* spp.), and numerous composites and legumes are common herbaceous plants.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Eastern redcedar is a dioecious species, and trees probably reach sexual maturity at about 10 years. Staminate strobili or conelets begin to develop on male trees at the tips of axillary branches of new scale-leaves. Pollen grains are formed by late September in conelets having 10 to 12 entire-margined sporophylls. Staminate strobili turn a conspicuous yellowish brown when they reach maturity during winter, and thus male trees are readily distinguished from ovulate ones.

Small green conelets begin to develop by early fall or late summer on ovulate trees but grow very little during the winter. They are borne terminally on axillary branches of the new scale-leaves but do not become conspicuous until late February to early spring. At this time the microsporangial walls of the staminate conelets split longitudinally, discharging the mature pollen. Pollen grains lodge at the end of the micropyle of the many ovules in the conelet. Pollination is complete in a few days when the conelet closes.

Growth of the pollen tube is slow at first but becomes active by late May or mid-June. Fertilization occurs in June and the mature embryo is full grown in about 2 months, anytime from late July to mid-November, depending on location. As the ovulate cone develops, greenish fruit-scales form the outer fleshy protective coat of the berrylike cone. Cones change color from green to greenish white to whitish blue and finally to bluish as the season progresses.

Each cone or fruit contains one to four (occasionally more) rounded or angled brownish seeds, 2 to 4 mm (0.08 to 0.16 in) long, often with longitudinal pits. The seed coat has a thick and bony outer layer and a thin, membranous inner layer (*23,47*).

Seed Production and Dissemination—Mature eastern redcedar trees produce some seeds nearly every year, but good crops occur only every 2 or 3 years. The cones do not open and will remain on the tree through the winter, although many are eaten and dispersed by animals. Most remaining cones are dispersed in February to March. Mature fruits are usually collected in the fall by hand-stripping or shaking onto canvas. Seeds may be stored as dried fruits or cleaned seeds.

After fanning to remove leaves, twigs, and other debris, the seeds can be extracted by running the fruit through a macerator and floating the pulp and empty seeds away. Dried fruits should be soaked in water several hours before macerating. Since eastern redcedar fruits are resinous, they should be soaked in a weak lye solution for 1 or 2 days. The soaking helps separate the oily, resinous pulp from the seeds and aids further washing, flotation, and stratification. This treatment should be followed by thorough washing (*45*). The cleaned seeds are ready for use, or they can be dried to 10 to 12 percent moisture content for storage at –7° C (20° F) to 4° C (40° F). The number of cleaned seeds per kilogram ranges from 81,570 (37,000/lb) to 121,250 (55,000/lb) and averages 96,120 (43,600/lb) (*23*). If seeds are to be sown in the spring, they should be soaked in a citric acid solution (10,000 ppm) for 96-hours, placed in moist-warm stratification at 24° C (75° F) for 6 weeks, and finally placed in moist-cool stratification at 5° C (41° F) for 10 weeks. Germination is best if fresh seeds are used. If desired, dry, stored seeds may be sown in mid-July, which accomplishes moist-warm stratification, and the over-winter period accomplishes moist-cool stratification for early spring germination (*46*).

In nursery practice, eastern redcedar seeds are broadcast or sown in rows spaced 15 to 20 cm (6 to 8 in) apart in well-prepared seedbeds and covered with about 6 mm (0.25 in) of firmed soil or sand. Stratified seeds should be sown in the spring early enough to allow completion of germination before air temperatures exceed 21° C (70° F). Germination of stratified seed usually begins in 6 to 10 days after sowing and is completed in 4 to 5 weeks. Untreated seeds may be sown in the fall and mulched until germination during the second spring after planting (*23*); but when fruits are depulped, dried, and stored at –16° C (4° F), seeds germinate the first spring after summer sowing (*46*). Germination is epigeal.

Fruits are eaten by birds and other animals, which are important vectors for seed dissemination (*20*) Seeds that pass through animal digestive tracts and those that remain on the ground beneath the trees may germinate the first or second spring. Most of the natural germination of eastern redcedar seed takes place in early spring of the second year after dispersal.

Eastern redcedar may also be established by hand direct-seeding or machine-sowing *(29)*. Both hand and furrow seeding are successful when stratified seeds are used at the rate of 1.35 kg/ha (1.2 lb/acre). Seedling catch is best where the amount of litter has been reduced and hardwood competition has been completely removed. The rate of sowing may be adjusted to allow for variations in germinative capacity of the seeds and degree of competition control.

Seedling Development—Eastern redcedar seedlings grown in nurseries may be transplanted from seedling beds after 1 or 2 years. Spacing in transplant beds ranges from about 15 by 3 cm (6 by 1 in) to 20 by 5 cm (8 by 2 in), depending on locality. The age at which trees are outplanted varies from area to area. Generally, eastern redcedar is field planted as 2–0, 3–0, 1–1, 1–2, 2–1, or 2–2 stock (numbers refer respectively to growing seasons in seedling beds and transplant beds).

Survival and growth of planted stock can be improved by grading the seedlings just after lifting from the nursery beds. Seedlings that are relatively small, topheavy, oversized, damaged, diseased, or insect-infested are discarded *(37)*. Culling after lifting from transplant beds is usually 1 to 3 percent, compared to 5 to 20 percent from seedling beds. Eastern redcedar seedlings should have a stem diameter of at least 4.0 mm (0.16 in), but preferably 5.6 mm (0.22 in), at the ground line. It is also desirable for seedlings to have top green weights that are no more than 3 to 4 times heavier than the roots *(26,36)*. Seedlings having higher top-to-root ratios are more likely to die under environmental stress.

Survival of eastern redcedar plantations has been variable, with low survival being attributed to poor seedling quality, low site quality, and competition. If these factors are considered carefully, however, eastern redcedar plantations can be successfully established. One early plantation established from hand-pulled wildlings had 84 percent survival. In a Nebraska plantation, established with 2-0 seedlings from 204 sources of eastern redcedar and Rocky Mountain juniper, first-year survival averaged 95.1 percent. Four other plantations from these sources averaged more than 85 percent survival, although one in Oklahoma had only 19.7 percent *(11,38)*.

Most natural eastern redcedar regeneration takes place on relatively poor hardwood or pine sites, along fence rows, or in pastures that are not burned or mowed. Seedlings are commonly established in rather open hardwood stands, adjacent to older seed-bearing eastern redcedar trees, as a result of birds eating the fruit and subsequent deposition of seeds *(34)*. On very dry sites, most seedlings are found in crevices, between layers of limestone, and in other protected places where the microclimate is most favorable. Seedling development is relatively slow on these adverse sites, although eastern redcedar seedlings withstand drought rather well *(4,22)*. First-year seedlings do not produce much height growth but develop a long fibrous root system *(15)*. Plantings from 2-0 stock showed good growth in some areas, however, exceeding 45 cm (17.8 in) in height after one growing season *(38)*. If competition from an overstory is rather severe, eastern redcedar seedlings may not survive. Once established, however, eastern redcedar survives for extended periods under severe competition *(15,28)*. Eastern redcedar also competes very well in shelterbelts, where it is the most common natural reproduction *(43)*.

Vegetative Reproduction—Eastern redcedar does not reproduce naturally by sprouting or suckering, but the species may be propagated by grafting, by air-layering, or from cuttings *(6,15,33,44)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth rates of eastern redcedar depend largely on site quality, competition from other species, and stand density. These factors probably reflect competition for available soil moisture on most sites. Trees 20 to 30 years old are generally 5 to 8 m (18 to 26 ft) tall and 6 to 8 cm (2.3 to 3.0 in) in d.b.h. Mature trees are usually 12 to 15 m (40 to 50 ft) tall and 30 to 61 cm (12 to 24 in) in d.b.h. On good sites, trees may reach 37 m (120 ft) in height and 122 cm (48 in) in d.b.h. *(25)*.

Some of the earliest data on diameter growth in natural eastern redcedar stands is presented in table 2 *(3)*. Site classes mentioned are those described in table 1. Analysis of these data provided equations to compute the height-age relationships in table 3. The relation of height of dominant and codominant trees to d.b.h. and stand density was also determined, after pooling of data for age and site classes *(11)*. Height growth, a reflection of soil depth and fertility, increases with stocking density (fig. 3).

Other studies in Arkansas have shown that growth and yield are affected by stand density and hardwood competition. In a 45-year-old eastern redcedar stand, highest volume growth was obtained in unthinned stands from which hardwoods had been removed. Volumes averaged 1.96 m^3/ha (28 ft^3/acre) per year during a 14-year period. This was double the growth of stands where hardwoods were left. A stand con-

Table 2—Average annual diameter growth of dominant eastern redcedar by site class and stand density[1]

Stand character	Site class			
	I	II	III	IV
		mm		
Under-stocked	7.6	8.1	4.6	3.6
Well-stocked	—	8.1	4.3	3.0
Over-stocked	—	3.8	2.5	1.8
		in		
Under-stocked	0.30	0.32	0.18	0.14
Well-stocked	—	0.32	0.17	0.12
Over-stocked	—	0.15	0.10	0.07

[1] Based on increment core measurements of 456 trees (3).

Table 3—Total height of eastern redcedars by age[1] and site class

Growth rings	Site class			
	II		III	
	m	*ft*	*m*	*ft*
10	4.6	15	3.7	12
15	5.5	18	5.2	17
20	7.6	25	6.1	20
25	8.5	28	7.3	24
30	9.8	32	7.9	26
35	10.7	35	8.8	29
40	11.3	37	9.4	31
45	12.2	40	10.1	33
50	12.8	42	10.7	35

[1] Age was computed using the total number of growth rings; false rings make accurate determinations difficult.

taining 432 crop trees per hectare (175/acre), 7.6 cm (3.0 in) d.b.h. and larger grew nearly the same volume after 14 years when 80 percent of the competition was removed as an unreleased stand of 988 trees per hectare (400/acre) *(11)*.

Over a 10-year period in northern Arkansas, completely released stands averaged higher growth in d.b.h., basal area, and volume than stands where only crown competition was removed. The greatest mean d.b.h. growth, 6.4 cm (2.5 in), occurred with the lightest stocking, 124 crop trees per hectare (50/acre). As stocking increased, mean d.b.h. growth decreased. Basal area increase was greatest in stands having 988 crop trees per hectare (400/acre), and as stocking decreased, basal area and volume growth decreased. An initial stocking of 988 eastern redcedar crop trees per hectare (400/acre), averaging about 7.6 cm (3 in) d.b.h., produced over 28 m^3/ha (2,000 fbm/acre) in 10 years. A stocking of 432 trees per hectare (175/acre), averaging 10.2 cm (4 in) d.b.h., produced slightly more volume during the same period on similar sites *(11)*.

On most sites eastern redcedar grows slowly, and long rotations are required to produce conventional sawlogs. Because the wood is used for small items, however, and there is wide latitude in acceptable defects, shortening of rotations and intermediate harvesting of merchantable wood are possible. About 20 to 30 years are required for posts and 40 to 60 years for sawtimber *(11,25)*.

Maintaining relatively dense stands can maximize post production. Thinning one or more times before harvest cut hastens sawlog production but may not increase total yield. The ideal density for growing sawlogs is not known, but excessive thinning may promote excessive formation of sapwood and growth of lower branches.

Rooting Habit—On shallow and rocky soils, eastern redcedar roots are very fibrous and tend to spread widely. Even first-year seedlings begin developing a long fibrous root system, often at the expense of top growth *(15)*. If soil conditions permit, eastern redcedar trees develop a deep, penetrating taproot.

Root development is greatly influenced by the size of soil-filled fissures. Eastern redcedar roots are known to grow extensively in soils in which limestone rocks make up more than 52 percent of the total soil volume *(11)* (fig. 4).

Reaction to Competition—Eastern redcedar has been classed as intolerant to very intolerant of shade *(11,30)*, but trees that have lived for decades beneath

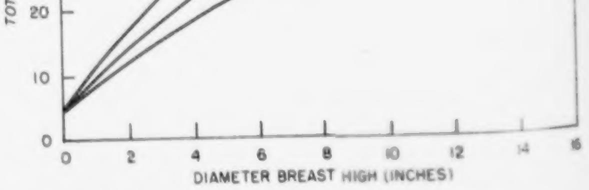

Figure 3—*Relation of height to d.b.h. by stocking class.*

a full canopy of hardwoods or pines on medium- to low-quality sites have been observed. Apparently, eastern redcedar has an inherent low capacity for water loss and the ability to sustain stomatal opening at low water potentials, which help the species adapt to dry environments *(4)*. Eastern redcedar can also conduct photosynthesis when overstory hardwoods are leafless and perhaps even reduces its light requirements for photosynthesis by adjusting to shaded conditions *(17,24)*. Eastern redcedar is a pioneer species on surface-mined areas (fig. 5), old fields, or pastures that are protected from fire; and it is the primary natural reproduction in many shelterbelts. However, stands formed through invasion of old fields may deteriorate at around 60 years of age as hardwoods or other competing species become established. Eastern redcedar grows well and faster than associated species because it is sun-adapted, drought-resistant, and has a long growing season. On most sites, eastern redcedar is temporary and is eventually replaced by more tolerant hardwoods and pines. However, clusters of eastern redcedar established beneath hardwoods have survived longer than the competing hardwood trees, possibly due to an allelopathic effect, or the species may be a better competitor for water and nutrients *(34)*. The species is more permanent on poor sites having thin, rocky soils, such as the glades of the Ozarks of Missouri and Arkansas and the Nashville Basin in central Tennessee. Eastern redcedar invasion of pastures is a problem on areas converted from poor hardwood sites in the Ozarks and western areas of its range *(9,31)*, and the species is likely to persist for a long time if left to grow *(7)*.

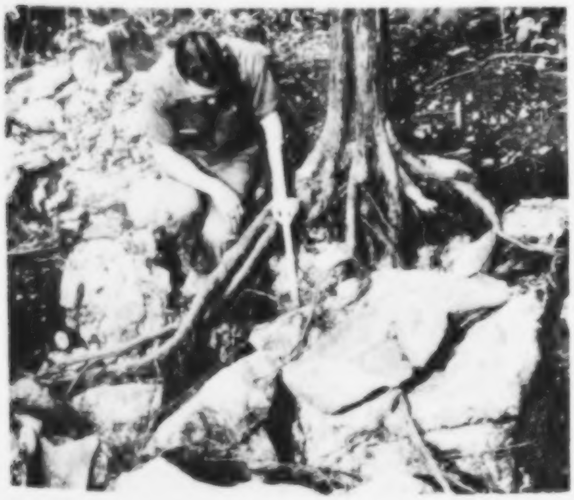

Figure 4—*Eastern redcedar root development in rocky soils.*

Eastern redcedar should be managed in even-aged stands, judging from studies conducted in northern Arkansas *(11)*. Good growth rates can be maintained by controlling competition and stand densities.

Damaging Agents—Fire is probably the worst enemy of eastern redcedar. The thin bark and roots near the ground surface are easily injured by fires. Some natural protection against fire exists because its foliage does not burn well and litter accumulation is minimal under stands on thin soils *(11,15)*.

Several insects damage eastern redcedar trees but rarely cause serious permanent damage *(5)*. Roots of seedlings are very susceptible to attack by nematodes and grubs. The foliage is eaten by bagworms *(Thyridopteryx ephemeraeformis)* and spruce spider mites *(Oligonychus ununguis)*, both of which can completely defoliate trees. The eastern juniper bark beetle *(Phloeosinus dentatus)* attacks the species but usually does not kill trees except when the attack is associated with the root rot fungus, *Heterobasidion annosum*. Another bark beetle *(Phloeosinus canadensis)* may feed on eastern redcedar. Several boring insects, including the black-horned juniper borer *(Callidium texanum)*, cedartree borer *(Semanotus ligneus)*, cypress and cedar borer *(Oeme rigida)*, and pales weevil *(Hylobius pales)* will attack eastern redcedar. The juniper midge *(Contarinia juniperina)* is a gall insect pest of redcedar which bores into the twigs at the base of needles and kills the portion beyond the entrance hole. In addition to pales weevil, two other weevils, the arborvitae weevil *(Phyllobius intrusus)* and the strawberry root weevil *(Otiorhynchus ovatus)*, feed on roots of eastern redcedar. The latter two weevils are also leaf feeders, along with the juniper webworm *(Dichomeris marginella)*; a wax moth *(Coleotechnites juniperella)*; a leaf roller *(Choristoneura houstonana)*, a pest of windbreak and ornamental plantings; and a sawfly *(Monoctenus mel-*

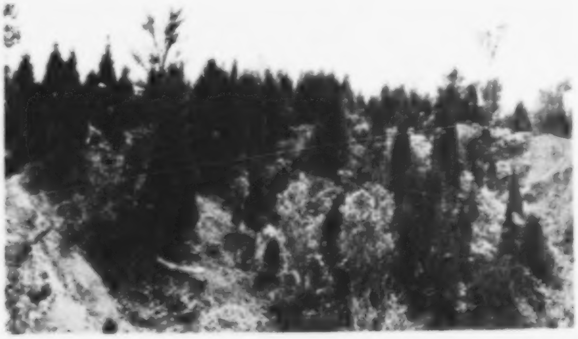

Figure 5—*Development of redcedar on surface-mined areas.*

liceps). The Fletcher scale *(Lecanium fletcheri)* and juniper scale *(Carulaspis juniperi)* are two other commonly occurring insects that attack junipers.

Eastern redcedar, especially when weakened by stress or insects, is very susceptible to damage by the root rot fungus, *Heterobasidion annosum*. This disease is thought to cause the greatest damage over much of its range. Cubical rot fungi *(Fomes subroseus* and *Daedalea juniperina)* and juniper pocket rot fungus *(Pyrofomes demidoffii)* enter eastern redcedars through dead branch stubs and attack the heartwood. Several other minor heart-rot fungi infect eastern redcedar *(21)*.

The major stem and foliage diseases of eastern redcedar are fungi known as cedar rusts in the genus *Gymnosporangium*. The most commonly known and widely spread species is cedar apple rust *(G. juniperi-virginianae)*, which attacks trees in all stages of development. Because it is an alternate host to this disease, the presence of redcedar is a problem to apple growers. Other common species are *G. clavipes*, *G. globosum*, *G. effusum*, and *G. nidus-avis*. The latter fungus is widely distributed and produces witches' brooms *(21)*. Important foliage diseases include Phomopsis blight *(Phomopsis juniperovora)* and *Cercospora sequoiae* blight, which also attack seedlings. Phomopsis blight has been difficult to control in nurseries, but newer developments show promise *(12,32)*. Both blights can cause major losses to eastern redcedar in the field, but Phomopsis blight is not a serious problem after seedlings reach age 4.

Newly established seedlings are subject to frost-heaving, and foliage may occasionally be damaged by winter injury *(23)*. Mice and rabbits may damage young eastern redcedar seedlings. Livestock generally avoid biting seedlings or trees but may trample the plants and their roots while grazing. During times of scarce food, deer will heavily browse eastern redcedar and destroy most reproduction *(11,20)*. Redcedar withstands the weight of snow fairly well, but it has only moderate resistance to ice damage *(8)*. Although the species is generally very tolerant to drought and temperature extremes, the author observed considerable mortality in west central Arkansas associated with the extremely hot, dry summer of 1980.

Special Uses

Eastern redcedar is important to wildlife. As an evergreen, it provides good nesting and roosting cover for many birds *(18,39)*. Dense thickets provide good escape cover for deer, and the abundant foliage, although low in quality, provides emergency food for them during times of stress. Fruits are high in crude fat and crude fiber, moderate in calcium, and very high in total carbohydrates. Eastern redcedar fruits are eaten by many wildlife species, including waxwings, bobwhite, quail, ruffed grouse, pheasant, wild turkeys, rabbits, foxes, raccoons, skunks, opossums, and coyotes *(20)*.

Eastern redcedar is among the best trees for protecting soils from wind erosion and reducing the desiccating effects of wind. It ranks high in the Great Plains shelterbelt plantings because of its ability to withstand extremes of drought, heat, and cold *(15)*. In Nebraska, eastern redcedar was the most suitable species among five combinations tested for single-row field windbreaks *(42)*. The fibrous root system also helps to hold soil in place, especially on shallow soils. Many varieties of eastern redcedar are used as ornamental plantings *(19,35)*. The species is also ranked among the top five for Christmas trees *(25)*. Eastern redcedar is also important as a source of cedarwood oil, which is a natural product for direct use in fragrance compounding or as a source of raw material producing additional fragrance compounds *(1)*.

Genetics

Population Differences

Eastern redcedar displays great diversity in phenotypic characteristics such as tree form, foliage color, and crown shape. Van Haverbeke's study *(41)* included a total of 43 gross morphological, foliage, cone, and seed characteristics and biochemical data derived from cone pulp. He points out that much of the research on morphological characteristics of eastern redcedar has been in the central and western parts of the species' range. More recently, however, information on genetic variation in natural stands in the eastern part of its range has been obtained *(13)*. Natural variation in the species may have been modified by past commercial exploitation of natural stands and by the selection, propagation, and distribution of clones *(47)*.

Races and Hybrids

Two distinct varieties have been recognized in the United States. *Juniperus virginiana* var. *crebra* (Fernald) is a northern form having a narrow crown and slightly pitted seeds. The other variety, *J. virginiana* var. *ambigens*, is an intermediate form between eastern redcedar and creeping juniper, *J. horizontalis* Moench *(15)*.

Although there are no recognized hybrids at this time, evidence is mounting that hybridization does occur. Population studies, especially in the western part of eastern redcedar's range, suggest that considerable introgression and perhaps blending of genetic differences have occurred whenever species' ranges overlap; and that *J. virginiana* readily hybridizes with *J. scopulorum*, *J. horizontalis*, and *J. ashei*, resulting in juniper populations that contain the germ plasm of two or three species *(15)*. Research in the Ozarks, however, showed no evidence of introgression into *J. ashei* by *J. virginiana* where *J. ashei* was surrounded by *J. virginiana (2)*.

The relatively strong influence of *J. scopulorum* germ plasm in the western part of the eastern redcedar population suggests that the entire population in the area studied is of hybrid origin *(41)*. This west-to-east flow of *J. scopulorum* germ plasm was further supported by Flake, Urbatch, and Turner *(14)*, who sampled many of Van Haverbeke's sample trees for terpenoid analysis. He proposed an alternative hypothesis that eastern redcedar of eastern and central North America may have been derived from the western juniper complex.

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Larix laricina (Du Roi) K. Koch **Tamarack**

Pinaceae Pine family

William F. Johnston

Tamarack *(Larix laricina)*, also called eastern, American, or Alaska larch, and hackmatack, is a small- to medium-sized deciduous conifer extending from the Atlantic to central Alaska. One of the largest tamaracks recorded is in Maine and measures about 94 cm (36.9 in) in d.b.h. and 29 m (95 ft) in height. The heavy, durable wood is used principally for pulpwood, but also for posts, poles, rough lumber, and fuelwood. Wildlife use the tree for food and nesting; it is also esthetically appealing and has significant potential as an ornamental.

Habitat

Native Range

Tamarack (fig. 1) has one of the widest ranges of all North American conifers. Its main range extends from Newfoundland and Labrador west along the northern limit of trees, and across the Continental Divide in northern Yukon Territory *(52)*; then south in the Mackenzie River drainage to northeastern British Columbia and central Alberta; and east to southern Manitoba, southern Minnesota, southern Wisconsin, extreme northeastern Illinois, northern Indiana, northern Ohio, northern Pennsylvania, northern New Jersey, northern Connecticut, and Maine. It also grows locally in the mountains of northern West Virginia and adjacent western Maryland. A major disjunct area of tamarack is found in interior Alaska, in the Yukon and Kuskokwim River basins between the Brooks Range on the north and the Alaska Range on the south; three minor areas are near the Alaska-Yukon border.

Climate

Because of its wide distribution, tamarack grows under extremely varied climatic conditions. Average January temperatures range from -30° to -1° C (-22° to 30° F) and those of July from 13° to 24° C (55° to 75° F). The lowest recorded temperatures range from -29° to -62° C (-20° to -79° F); the highest, from 29° to 43° C (85° to 110° F).

Annual precipitation within the range of tamarack is also extremely variable. It ranges from 180 mm (7 in) at Fort Yukon, AK, to 1400 mm (55 in) in eastern Canada. Of this, 75 to 355 mm (3 to 14 in) is in June, July, and August. Snowfall has a similarly wide variation, from about 100 cm (40 in) in the District of Mackenzie in northwestern Canada to 510 cm (200 in) near the Atlantic coast in Labrador and Quebec.

The average frost-free period for tamarack ranges from probably less than 75 days over much of its range to 120 days in interior Alaska and 180 days along its southern limits. The generally shorter growing season in the northern latitudes is counterbalanced by longer periods of daylight *(12)*.

Soils and Topography

Tamarack can tolerate a wide range of soil conditions but grows most commonly on wet to moist organic soils (Histosols) such as sphagnum peat and woody peat. The latter is usually better decomposed, has more nitrogen and mineral nutrients, and is less acid than sphagnum peat. Tamarack grows fairly well on extremely dry soils where these are shallow over bedrock or where the water table is low, but it can die from drought on such sites. The tree is found on mineral soils, especially Inceptisols and Entisols, that range from heavy clay to coarse sand; thus texture does not seem to be limiting. Although tamarack can grow well on calcareous soils, it is not abundant on the limestone areas of eastern Ontario *(27)* and is rare on those of the Gaspé Peninsula and Anticosti Island in Canada.

Because it can withstand high soil moisture, high acidity, and low soil temperature, tamarack is more abundant on peatlands than trees characteristic of surrounding uplands. It grows best, however, on more favorable sites such as moist but well-drained loamy soils along streams, lakes, and swamps; seep areas; and mineral soils with a shallow surface layer of organic matter *(12)*. In Alaska tamarack grows well on upland sites having wind-deposited loess soils *(50)*.

Tamarack is a characteristic tree of peatlands, especially in the southern limits of its range. It is found on the full range of peatlands from rich swamp (forested rich fen) to raised bog but is most characteristic of poor swamps where the soil water is weakly enriched with mineral nutrients *(17)*. Farther north tamarack is still common on peatlands *(38)*; in Alaska it occurs especially on bogs underlain by permafrost (perennially frozen soils) *(50)*.

Tamarack often grows on much drier sites in the northern part of its range. Scattered individuals and

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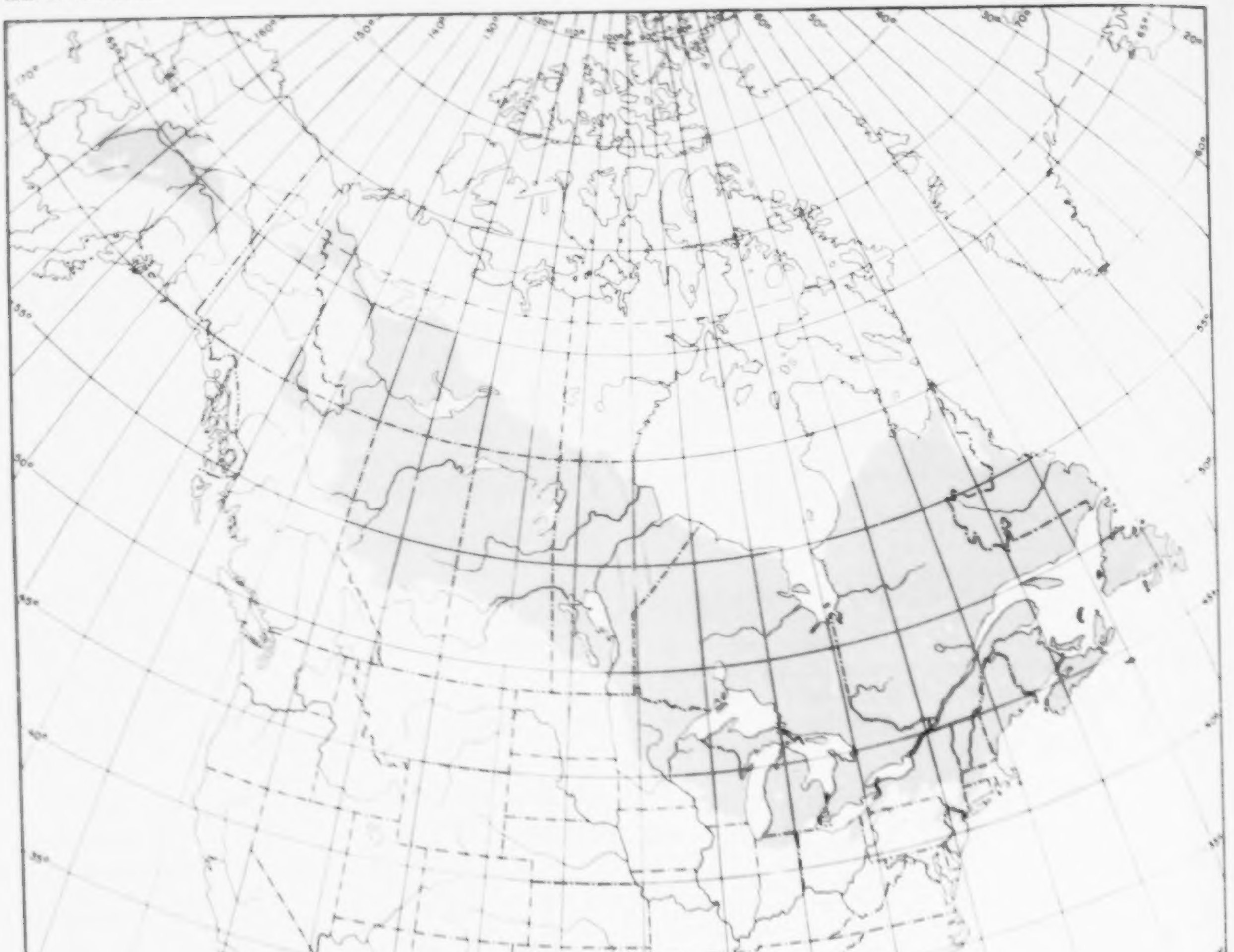
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Figure 1—*The native range of tamarack.*

sometimes stands are found on swamp margins, on the banks of streams and lakes, and on low ridges and benches and other upland sites. In the Hudson Bay lowlands, tamarack grows on both extensive fens *(11)* and beach ridges *(38)*. In British Columbia it is often an upland tree, growing on the cool moist north slopes of mountains as well as in valley swamps.

Tamarack grows on sites with about the same elevation throughout most of its range. In eastern North America, however, the tree grows between sea level and 1220 m (4,000 ft); in the Canadian Rockies and Alaska it grows between about 180 and 520 m (600 and 1,700 ft) *(12)*.

Associated Forest Cover

Tamarack forms extensive pure stands in the boreal region of Canada and in northern Minnesota. In the rest of its United States range and in the Maritime Provinces tamarack is found locally in both pure and mixed stands. It is a major component in the forest cover types Tamarack (Society of American Foresters Type 38) and Black Spruce–Tamarack (Type 13) and is a minor component in the following types *(11)*:

1	Jack Pine
5	Balsam Fir
12	Black Spruce
33	Red Spruce–Balsam Fir
37	Northern White-Cedar
39	Black Ash–American Elm–Red Maple
107	White Spruce
203	Balsam Poplar
204	Black Spruce
253	Black Spruce–White Spruce
254	Black Spruce–Paper Birch

Black spruce *(Picea mariana)* is usually tamarack's main associate in mixed stands on all sites. The other most common associates include balsam fir *(Abies balsamea)*, white spruce *(Picea glauca)*, and quaking aspen *(Populus tremuloides)* in the boreal region, and northern white-cedar *(Thuja occidentalis)*, balsam fir, black ash *(Fraxinus nigra)*, and red maple *(Acer rubrum)* on the wetter organic-soil (swamp) sites in the northern forest region *(11)*. In Alaska, quaking aspen and tamarack are almost never found together *(50)*. Additional common associates are American elm *(Ulmus americana)*, balsam poplar *(Populus balsamifera)*, jack pine *(Pinus banksiana)*, paper birch *(Betula papyrifera)*, Kenai birch *(B. papyrifera* var. *kenaica)*, and yellow birch *(B. alleghaniensis)*.

Tamarack stands cast light shade and so usually have a dense undergrowth of shrubs and herbs. Because the tree has an extensive range, a great variety of shrubs is associated with it. Dominant tall shrubs include dwarf (resin) and low (swamp) birch *(Betula glandulosa* and *B. pumila)*, willows *(Salix* spp.), speckled alder *(Alnus rugosa)*, and red-osier dogwood *(Cornus stolonifera)*; low shrubs include Labrador-tea *(Ledum groenlandicum)*, bog-rosemary *(Andromeda glaucophylla)*, leatherleaf *(Chamaedaphne calyculata)*, and small cranberry *(Vaccinium oxycoccos)* (see *12* for a more complete list). Characteristically the herbaceous cover includes sedges *(Carex* spp.), cottongrass *(Eriophorum* spp.), false Solomonseal *(Smilacina trifolia)*, marsh cinquefoil *(Potentilla palustris)*, marsh-marigold *(Caltha palustris)*, and bogbean *(Menyanthes trifoliata)*. Ground cover is usually composed of sphagnum moss *(Sphagnum* spp.) and other mosses *(11)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Tamarack is monoecious; male and female flowers are small, solitary, and appear with the needles. Male flowers are yellow, globose, and are borne mainly on 1- or 2-year-old branchlets. Female flowers are reddish, subglobose, and are borne most commonly on 2- to 4-year-old branchlets, but also on branchlets 5 to 10 or more years old, or on 1-year-old twigs of young trees. Cones usually are produced on young growth of vigorous trees. On open-grown trees, cones are borne on all parts of the crown. Ripe cones are brown, oblong-ovoid, and 13 to 19 mm (0.50 to 0.75 in) long.

General dates for tamarack flowering in Ontario and the Lake States are April to May *(36)*, especially from late April to early May *(1,12)*. In interior Alaska tamarack generally flowers from mid- to late May *(50)*. General dates for cone ripening in Ontario and the Lake States are August to September.

Seed Production and Dissemination—Isolated trees on peatlands and trees in upland plantations begin to bear viable seed at 12 to 15 years of age or even less. In eastern Ontario viable seed has been collected from vigorous plantations as young as 4 years *(27)*. Seed production in large quantities generally begins at about 40 years, the optimum age being about 75 years. Tamaracks on peatland in Saskatchewan and Manitoba do not bear cones in quantity, however, until they are about 50 years old *(12)*.

Vigorous, open-grown trees 50 to 150 years old produce the best cone crops; a single tree may bear as many as 20,000 cones containing more than 300,000 full seeds in a good year. Seed production in stands is generally confined to dominant and codominant trees. Open-grown mature stands 80 years old may produce 3,700,000 to 6,200,000 full seeds per hectare (1,500,000 to 2,500,000/acre) in a good year, while closed stands the same age may produce 1,200,000 to 3,000,000 seeds per hectare (500,000 to 1,200,000/acre).

Tamarack bears good seed crops at intervals of 3 to 6 years, with some seed produced in intervening years. In Minnesota cones from mature trees averaged 26 seeds, 67 percent of which were full; cones from young trees averaged 39 seeds and 85 percent were full.

General dates for tamarack seed dispersal in Ontario, the Lake States, and interior Alaska are September to spring *(36,50)*. A 1-year study in northeastern Minnesota revealed that 65 percent of the crop fell from September 1 to September 20, 25 percent from September 20 to October 10, and nearly all of the remaining 10 percent before October 31. Empty cones remain on the trees from 2 to 5 years *(12)*.

Tamarack seeds are 3 mm (0.12 in) long and have light chestnut-brown wings 6 mm (0.25 in) long; cleaned seeds average about 550 000 to 710 000/kg (250,000 to 320,000/lb) *(18,36)*. Although the seeds are small, few fall at a distance greater than twice the tree height. However, tamarack can reproduce well as far as 60 m (200 ft) from seed-bearing trees if favorable seedbeds are present *(22)*.

Seedling Development—Up to half the tamarack seeds that fall may be destroyed by rodents. As a result of this loss plus that by fungi or bacteria, only 4 to 5 percent of the seed may germinate *(22)*. In nurseries, erratic and often poor germination has been a major difficulty in producing tamarack stock *(27)*; germination can even be poor in a greenhouse *(34)*. Recleaning the seed can substantially reduce the high percentage of empty or improperly developed seed found in many seed lots *(16)*. Experience in Ontario shows that under optimum conditions, seed collected from vigorous stands in a good seed year has 75 to 90 percent germination *(27)*.

Tamarack seed remains viable for 4 years or more when stored in sealed containers at 4 to 6 percent moisture content and -8° to -6° C (18° to 22° F). Internal dormancy apparently ranges from none to mild. Under forest conditions any existing dormancy is broken while the seed lies on the ground during the first winter; thus fall sowing is generally recommended. However, spring-sown seed may germinate well without any cold stratification *(18,36)*.

Germination is epigeal, the cotyledons rising above the ground. It normally begins from late May to mid-June and reaches a peak at surface temperatures of 18° to 21° C (65° to 70° F). In laboratory experiments germination has occurred at temperatures as low as 12° C (54° F) *(4)* and the rate may increase with temperature up to about 24° C (75° F). Under deep shade germination occurred at 13° C (55° F). Alternating day and night temperatures of 30° and 20° C (86° and 68° F), respectively, are recommended for germination tests *(36)*.

The best seedbed is warm, moist mineral or organic soil with no brush but a light cover of grass or other herbaceous vegetation. Hummocks of slow-growing sphagnum moss often make a good seedbed, but some sphagnum mosses may offer too much competition. In Minnesota germination beneath tamarack stands was best on fine-textured mosses (primarily *Mnium*, *Drepanocladus*, and *Helodium*) *(12)*. Findings from clearcut peatlands in Minnesota show that slash-burned seedbeds favor tamarack reproduction, whereas slash hinders it *(22)*. On uplands, tamarack apparently reproduces well on rock-raked areas after natural seeding.

For best growth tamarack seedlings need abundant light and a constant but suitable water level. In Canadian studies, full light produced the tallest seedlings and heaviest root weights *(26)*. Under drought conditions, leader length and stem diameter were significantly reduced by soil moisture tensions of 15.2 bar (15 atm), but tensions of 1.0 and 6.1 bar (1 and 6 atm) had little effect *(14)*. Seedlings under fully stocked stands usually grow 2 to 3 cm (1 in) the first year and do not survive beyond the sixth year. With little or no cover they may be as tall as 18 to 23 cm (7 to 9 in) the first year and 46 to 64 cm (18 to 25 in) the third year. From then on, growth is generally even more rapid if light is adequate and drainage is good *(12)*.

Buds begin to swell 2 or 3 weeks before opening; in northeastern Minnesota this occurs from early to late April. Needles begin to emerge from about mid-April to mid-May in Minnesota, Michigan's Upper Peninsula, and Saskatchewan. On the short shoots, needles elongate rapidly and the annual stem increment—only about 1 mm (0.04 in)—is completed shortly after budbreak. On the long shoots, bud needles reach full length by mid- to late June in northern Wisconsin, whereas stem needles mature along the stem as it grows; stem elongation is completed by the end of July *(6)*. Needles begin to turn yellow in early September in Michigan's Upper Peninsula and reach maximum color in early October in Michigan and northeastern Minnesota. Tamarack loses its needles in these same areas from about mid-September to mid-October *(1,12)*.

Height growth apparently does not begin until the first needles are fully developed. In Michigan's Upper Peninsula height growth begins in late May and continues until mid-August (*12*). Diameter growth begins from early April to early June and ceases from late July to early August in northeastern Minnesota (*1*).

Because they are small, tamarack seedlings are easily killed during the first 6 or 8 weeks after germination. Early losses are primarily caused by damping-off; in the second and third years drought, drowning, and inadequate light sometimes cause appreciable loss. One-year-old seedlings grown in full light can survive desiccation of the upper 2 to 3 cm (1 in) of organic soils to as low as 45 to 65 percent by weight, whereas forest-grown seedlings 1 to 3 years old are fairly intolerant of drought (or flooding) (*12*).

Vegetative Reproduction—*Layering is apparently the dominant reproductive mode for tamarack along the northern limit of trees in Canada and Alaska (10,50), whereas farther south it is uncommon but may occur when branches are covered by fast-growing sphagnum moss or drifting sand.* Roots are also known to produce shoots (*12*), and experience in Ontario shows that tamarack can be easily propagated from softwood cuttings taken in early July from young trees (probably less than 5 to 7 years old) (*27*).

Sapling and Pole Stages to Maturity

Growth and Yield—Average heights of mature trees are 15 to 23 m (50 to 75 ft), but occasional individuals may grow 30 to 35 m (100 to 115 ft) tall. Mature trees are usually 36 to 51 cm (14 to 20 in) in d.b.h., but a few reach 61 to 100 cm (24 to 40 in). Trees 18 to 24 m (60 to 80 ft) tall and 51 to 61 cm (20 to 24 in) in d.b.h. were once common in the Lake States. In interior Alaska, mature tamaracks often are only 3 m (10 ft) tall and 8 cm (3 in) in d.b.h. (*50*); on good sites, however, they sometimes reach heights of 24 to 27 m (80 to 90 ft) and diameters of 30 to 38 cm (12 to 15 in) (*50*). Maximum age is generally 150 to 180 years, but trees 230 to 240 years old and one 335-year-old individual have been found.

The growth rate of tamarack apparently depends on both the nutrient status and moisture-aeration conditions of the site. In Minnesota, tamarack site index is positively correlated to nutrient supply and foliar nutrient concentrations (especially nitrogen and phosphorus) but negatively correlated to amount of standing water (*48*). On water-covered stagnant peatlands, the tree grows slowly and may be only 2 m (6 ft) tall in 55 years. In northern Ontario it grows well on 91 cm (36 in) or more of peat if the zone of continuous saturation is at a depth of 46 cm (18 in) or more (*55*); drainage of tamarack-speckled alder swamps in the clay belt would probably increase site index (at 100 years) by about 3 m (10 ft) (*30*).

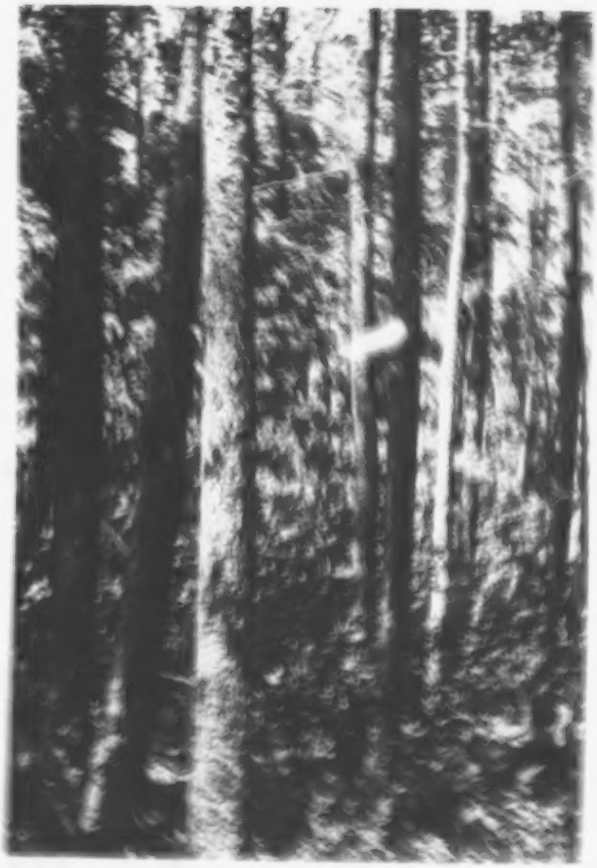

Figure 2—*A polesized stand of tamarack on a good peatland site in northern Minnesota.*

With abundant light, tamarack is one of the fastest growing conifers on uplands in the boreal (including Alaska) and northern forest regions; on peatlands it outgrows any other native conifer (*6,12,50*). In Alberta, good-site tamarack averages almost 0.5 m (1.5 ft) in annual height growth for 20 to 30 years, but growth apparently drops sharply when the crowns close, or after the age of 40 to 50 years.

Information on growth of natural tamarack stands is apparently available only from northern Minnesota (fig. 2). Limited data indicate that annual growth of poletimber stands (presumably on peatland sites) is from 1.9 to 2.5 m^3/ha (0.3 to 0.4 cord/acre). In 70- to 100-year-old stands, annual periodic growth averaged 3.8 m^3/ha (0.6 cord/acre) on well-stocked plots with a basal area of 21 m^2/ha (93 ft^2/acre) and 1.9 m^3/ha (0.3 cord/acre) on poorly stocked plots with 8 m^2/ha (35 ft^2/acre) *(12)*.

No yield tables are known for tamarack. Characteristics of a few 80- to 130-year-old stands on medium- to poor-peatland sites in northern Minnesota generally ranged as follows: average height, 12.2 to 15.5 m (40 to 51 ft); average d.b.h., 13.0 to 14.7 cm (5.1 to 5.8 in); number of trees, 1,370 to 1,740/ha (555 to 705/acre); and basal area, 19 to 23 m^2/ha (83 to 102 ft^2/acre) *(41)*.

No doubt because of its potential for rapid juvenile growth, tamarack has been used in several planting tests on different sites in the Lake States *(25,32,33)* and eastern Canada *(15,28)*. Trees grew slowly on peatland, but on other sites height averaged from 3.2 to 4.4 m (10.5 to 14.4 ft) in 8- to 10-year-old plantations where competing vegetation was initially controlled. Survival was more variable, being very poor on shallow soils over limestone.

Growth rate (particularly diameter) declines after 12 to 15 years if tamarack is planted at close spacings such as 1.5 by 1.5 m (5 by 5 ft), but it should be unimpeded for the first 25 years at wider spacings up to 2.4 by 2.4 m (8 by 8 ft). In a good plantation in eastern Ontario, height at 25 years averaged 14.9 m (49 ft), d.b.h. 17.3 cm (6.8 in), and volume 202 m^3/ha (32 cords/acre). Depending on site, final harvests of 189 to 252 m^3/ha (30 to 40 cords/acre) are possible at 25 years in well-managed tamarack plantations *(27)*. Intensively cultured plantations can produce two to three times more biomass than conventionally tended stands *(5)*.

In stands tamarack is characteristically a straight, slender tree with a narrow, pyramidal crown that occupies one-third to one-half the bole length (fig. 5). Trees whose tops have died back after heavy defoliation by the larch sawfly (*Pristiphora erichsonii*) or after prolonged flooding typically produce numerous adventitious shoots. Although these shoots no doubt help tamarack survive defoliation or flooding, they also apparently support high sawfly populations *(12)*.

Rooting Habit—Tamarack typically has a shallow, spreading root system. On favorable sites roots may spread over an area greater in radius than the tree height but are only 30 to 61 cm (12 to 24 in) deep. Trees on sandy upland have a platelike rooting habit; few roots reach below a 30-cm (12-in) depth and taproots are rare. On wet sites tamarack roots are usually stringy with no branches on the terminal 15 cm (6 in). Peatland tamaracks, in particular, have

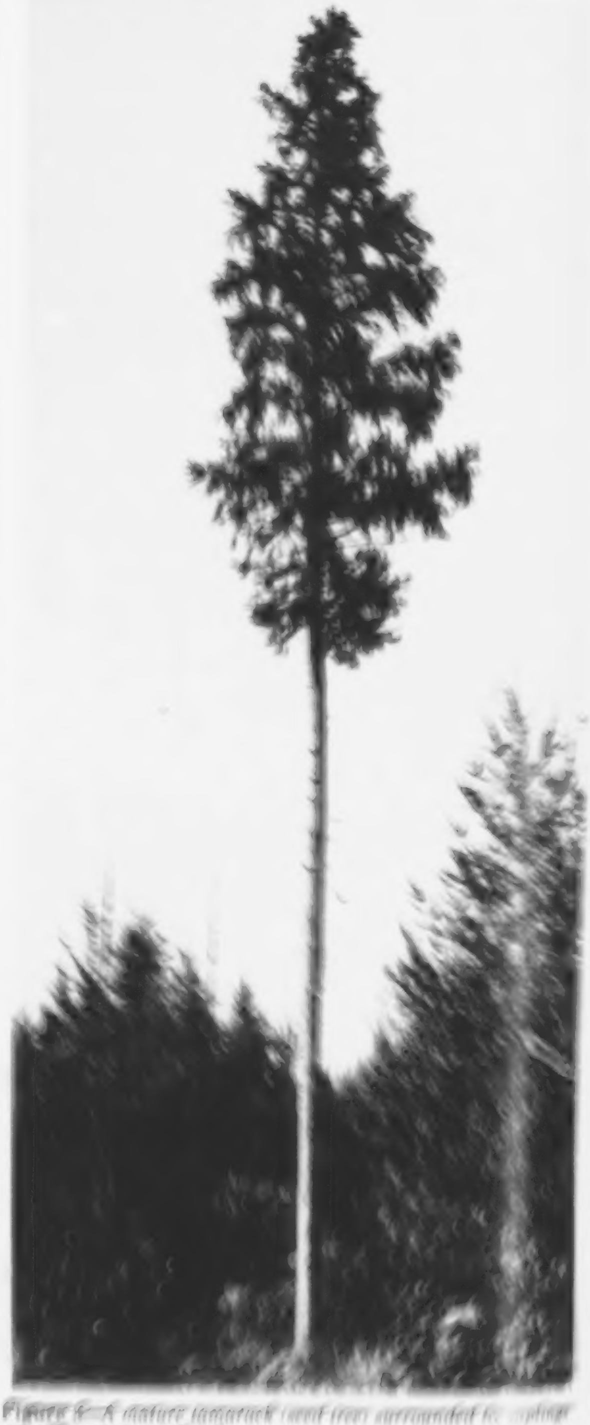

Figure 5—A mature tamarack (seed tree) surrounded by saplings on a Minnesota peatland.

wide root systems and do not form taproots. As the moss layer deepens, new roots develop on the stem above the original root collar, and growth of old roots nearly ceases. On drier sites roots of larger trees bend sharply from the trunks, forming knees *(12)*.

Reaction to Competition—Tamarack is very intolerant of shade. Although it can tolerate some shade during the first several years *(21,50)*, it must become dominant to survive, and when mixed with other species, it must be in the overstory. On good swamp sites in Michigan, for example, tamarack is a dominant tree in the overstory of some mixed conifer stands, but it is practically never found in the understory *(2)*. The tree is a good self-pruner, and boles of 25- to 30-year-old trees may be clear for one-half or two-thirds their length.

Tamarack is a pioneer tree, especially on open unburned bogs and burned organic soil *(11)*. It is generally the first forest tree to invade filled-lake bogs. In the Lake States tamarack may first appear in the sedge mat, sphagnum moss, or not until the bog shrub stage; farther north it is the pioneer tree in the bog shrub stage *(12)*. Tamarack is fairly well adapted to reproduce successfully on burns *(35)*, so it is one of the usual pioneers on most sites in the boreal forest immediately after fire. The tree commonly forms stands on abandoned farmland in eastern Ontario *(27)* and reproduces well on sites in Alaska that were cleared and then abandoned *(50)*.

Because tamarack is very intolerant, it does not become established in its own shade. Consequently, the more tolerant black spruce eventually succeeds tamarack on poor (bog) sites, whereas northern white-cedar, balsam fir, and swamp hardwoods succeed tamarack on good (swamp) sites *(12)*. Recurring sawfly outbreaks throughout the range of tamarack have probably speeded the usual succession to black spruce or other associates *(9)*.

Various tests on planting and natural reproduction indicate that competing vegetation hinders tamarack establishment. A year's delay in planting furrows on a wet lowland resulted in significantly lower first-year survival, apparently because of the rapid resurgence of grass and other herbaceous vegetation *(24)*. On brushy peatland, 7-year survival and height were both much lower where tamarack was planted on unsprayed rather than on herbicide-sprayed areas *(44)*. Six years after broadcast burning and natural seeding on peatland, tamaracks overtopped by surrounding vegetation were only about half as tall as those generally not overtopped *(21)*. Tamarack does not grow well where sugar maple (*Acer saccharum*) reproduction is present; this seems at least partly due to the maple's root exudate *(44)*.

The intolerance of tamarack dictates the use of even-aged management, with some adaptation of clearcutting or seed-tree cutting generally considered the best silvicultural system, because tamarack seeds apparently germinate better in the open and the seedlings require practically full light to survive and grow well. Tamarack is also usually windfirm enough for the seed-tree system to succeed (fig. 3). Satisfactory reestablishment of tamarack, however, often requires some kind of site preparation, such as slash disposal and herbicide spraying *(22)*.

For successful tamarack plantations, the planting stock's roots and shoots must be well balanced and dormant; probably the best stock is begun in a greenhouse and transplanted for 1 year. Competition must also be controlled, the first 2 years after planting being critical. Because tamarack is very intolerant, the trees should be planted at wide spacings such as 2.4 by 2.4 m (8 by 8 ft) *(27)*.

Damaging Agents—Because its bark is thin, tamarack is highly susceptible to fire damage, except perhaps in older, upland stands; and because its roots are shallow, it is usually killed on peatlands by all but very light burns. However, the habitat of tamarack—especially south of the boreal forest—is normally wet enough to protect the tree from fire *(6)*. In the boreal forest the tamarack type apparently has a high surface-fire hazard in spring but a low crown-fire hazard in pure stands *(35)*.

Abnormally high water levels often kill tamarack stands, and those that survive under such conditions usually grow very slowly. Other effects of high water include dieback and the development of adventitious roots and shoots *(8)*. Wetland road crossings and beaver damming are the primary causes of flooding. Road-caused flooding has killed tamarack or reduced its growth on thousands of hectares in northern Minnesota *(40)*; natural gas and petroleum pipelines will probably have similar effects unless cross drainage is provided *(3)*.

Strong winds can uproot large tamarack trees growing in swamps or other wet sites where rooting is shallow. Compared with black spruce, however, tamarack seems to be fairly windfirm.

The larch sawfly is the most destructive insect enemy of tamarack. Epidemics occur periodically across Canada and the northern United States and have caused tremendous losses of merchantable tamarack throughout most of the tree's range. Indications are that radial increment declines markedly after 4 to 6 years of outbreak and trees die after 6 to 9 years of moderate to heavy defoliation *(9)*. In southeastern Manitoba and northern Minnesota, however, imported parasites of the sawfly (especially

Olesicampe benefactor) have become established and should reduce the frequency and duration of future outbreaks (*42*).

The larch casebearer (*Coleophora laricella*) is also a serious defoliator of tamarack. A native of Europe, it is now widely distributed in eastern North America westward to southeastern Manitoba and the Lake States. The larch casebearer attacks tamarack of all ages, and several severe outbreaks have caused extensive mortality in some areas (*49*). Outbreak severity has lessened in recent years, however, probably because imported parasites of the casebearer have also become widely established (*34*).

Only a few other insects and related organisms (such as mites) that feed on tamarack are known to sometimes cause serious injury. During an outbreak the spruce budworm (*Choristoneura fumiferana*) can severely damage tamarack where it grows along with balsam fir and white spruce—the preferred hosts. The larch bud moth (*Zeiraphera improbana*) has had occasional short epidemics, and the spruce spider mite (*Oligonychus ununguis*) is occasionally found in large numbers on tamarack. The larch shoot moth (*Argyresthia laricella*) is widely distributed but serious injury is unusual. One of the most common bark beetles attacking tamarack is the eastern larch beetle (*Dendroctonus simplex*), but it feeds mainly on weakened, dying, or dead trees. Warren's collar weevil (*Hylobius warreni*), common in Canada, has killed pole-sized tamarack in Michigan's Upper Peninsula (*34,49*).

Several insects feed on tamarack cones and seeds, but little is known about their importance. Those that feed inside cones include the spruce coneworm (*Dioryctria reniculelloides*) and a seed chalcid (*Megastigmus laricis*). Two defoliators that sometimes feed on tender young cones during epidemics are the spruce budworm and the larch bud moth (*16,34*). Cones were still being produced after 3 to 4 years' defoliation by the larch sawfly in Canada and after 8 years of attack in northern Minnesota (*12*).

Tamarack is host to many pathogens, but none causes disease serious enough to have an economic impact on its culture. The only common foliage diseases are rusts, such as the leaf rust of poplar (*Populus* spp.) and larch (*Larix* spp.) in eastern and central North America. However, this rust, caused by the fungus *Melampsora medusae*, and other rusts do little damage to tamarack (*19,37*). The needle-cast fungus *Hypodermella laricis* has attacked tamarack in Ontario and has the potential for local damage.

Tamarack is essentially free of stem diseases. Eastern dwarf mistletoe (*Arceuthobium pusillum*) is occasionally found on the tree (*29*), but its witches' brooms are small on tamarack and occur only where the tree is growing in mixture with infected black spruce (*19*).

The root- and butt-rot fungi reported on tamarack include Armillaria (or shoestring) root rot (*Armillaria mellea*), *Scytinostroma galactinum*, red-brown butt rot (*Phaeolus schweinitzii*), and the false velvet top fungus (*Inonotus tomentosus*) (*19,47*). They are not aggressive killers on tamarack; however, flood-damaged trees are particularly susceptible to attack by fungi such as Armillaria root rot (*8*), and pole-sized trees have been killed by the false velvet top fungus.

The principal heart-rot fungi of tamarack are brown trunk rot (*Fomitopsis officinalis*) and red ring rot (*Phellinus pini*). *Climacocystis borealis* causes a white mottled rot of tamarack in Canada (*19*).

Snowshoe hares kill many tamarack seedlings in some areas of the Lake States, Alberta, and Alaska (*50*). White-tailed deer and moose apparently browse seedlings or saplings to a lesser extent. Porcupines commonly feed on the inner bark and deform the stem or kill the tree. Many tamarack stands have been damaged by this pest in the Lake States, Maine, and eastern Canada (*27*). It can be especially damaging in plantations (*48*). Red squirrels often cut cone-bearing branchlets, and birds such as the red crossbill occasionally eat the seeds (*12*).

Special Uses

The principal commercial use of tamarack in the United States is for making pulp products, especially the transparent paper in window envelopes. Because of its rot resistance, tamarack is also used for posts, poles, mine timbers, and railroad ties. Other wood products include rough lumber, fuelwood, boxes, crates, and pails (*23*). In interior Alaska young tamarack stems are used for dogsled runners, boat ribs, and fishtraps (*4*); in northern Alberta the branches are used to make duck and goose decoys (*50*). Historically, knees from larger trees were used in wooden ship construction and Indians used the fine roots to sew birch bark, the wood for arrow shafts, and the bark for medicine (*48*).

Tamarack has certain wildlife values. Porcupines feed on the inner bark, snowshoe hares browse on seedlings, and red squirrels eat the seeds. Birds common in tamarack stands during the summer include the white-throated sparrow, song sparrow, veery, common yellowthroat, and Nashville warbler (*7*). The American osprey, a sensitive species, often nests in lowland types such as tamarack; and the great gray owl, a rare winter visitor in the northern Lake States, apparently nests there only in the tamarack peatlands of northern Minnesota.

Tamarack is esthetically appealing, especially in early autumn when its needles turn yellow. Although the tree has been infrequently planted for ornamental purposes *(30)*, it has significant potential—even in Alaska *(50)*—because of its rapid growth and fall color. Tamarack is particularly valuable in suburban areas but is not suitable as a shade tree on city streets *(18)*.

Tamarack has limited value as a watershed protector because it usually grows on gently sloping terrain, and management of the type probably has little or no effect on water yield or quality because harvesting is generally on a small scale.

Genetics

Population Differences and Races

Tamarack shows much genetic variation. Growth responses to photoperiod were found to differ between northern seed sources and a southern source *(45)*. Differences in germination patterns due to photoperiod and length of cold stratification have been shown between seed from interior Alaska and seed from southern sources *(4)*.

Growth responses would seem to indicate that photoperiodic ecotypes exist in tamarack *(45)*. The species is considered to have a clinal pattern of variation, however, and no races or ecotypes are presently recognized. For example, tamarack's gene pool in Wisconsin is highly variable but unsegmented, with a clinal pattern of variation evident among the State's major geographic subdivisions *(31)*.

Tamarack seed sources differed significantly in survival, height, and d.b.h. 10 years after planting in north-central Wisconsin. The following sources grew best on a high-yield site and are recommended for north-central Wisconsin *(32)*: Somerset County, ME; Eau Claire, La Crosse, and Oneida Counties, WI; and Annapolis County, NS.

Tamarack in Alaska was once named as a separate species *(Larix alaskensis)* and later reduced to a variety *(L. laricina* var. *alaskensis)*, but the Alaska variety is no longer accepted *(46)*.

Hybrids

Little information is available on intraspecific hybridization in tamarack, but careful selection and breeding may result in substantial genetic improvement. Similarly, although tamarack has been little used in interspecific hybridization, it has been crossed with two other species of the Section *Pauciseriales*—Japanese larch *(Larix leptolepis)* and European larch *(L. decidua)*. Progenies with hybrid vigor are often produced, but seed yield is very low *(13)*. The tamarack-Japanese larch hybrid is especially promising because it combines rapid growth with adaptability to shorter growing seasons *(20)*. Although crosses between tamarack and the remaining species of the Section—Dahurian larch *(L. gmelini)* and Siberian larch *(L. sibirica)*—seem feasible *(30)*, apparently none has yet been produced.

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Larix lyallii Parl. **Alpine Larch**

Pinaceae Pine family

Stephen F. Arno

Alpine larch (*Larix lyallii*), also called subalpine larch and Lyall larch, is a deciduous conifer. Its common name recognizes that this species often grows higher up on cool exposures than any other trees, thereby occupying what would otherwise be an alpine tundra. Both early-day botanical explorers and modern visitors to the high mountains have noted this tree's remarkable ability to form pure groves above the limits of evergreen conifers. Alpine larch inhabits remote high-mountain terrain and its wood has essentially no commercial value; however this tree is ecologically interesting and esthetically attractive. Growing in a very cold, snowy, and often windy environment, alpine larch usually remains small and stunted, but in windsheltered basins it sometimes attains large size—maximum 201 cm (79 in) in d.b.h. and 29 m (95 ft) in height. This species is distinguished from its lower elevation relative western larch (*Larix occidentalis*) by the woolly hairs that cover its buds and recent twigs, and frequently by its broad, irregular crown.

Habitat

Native Range

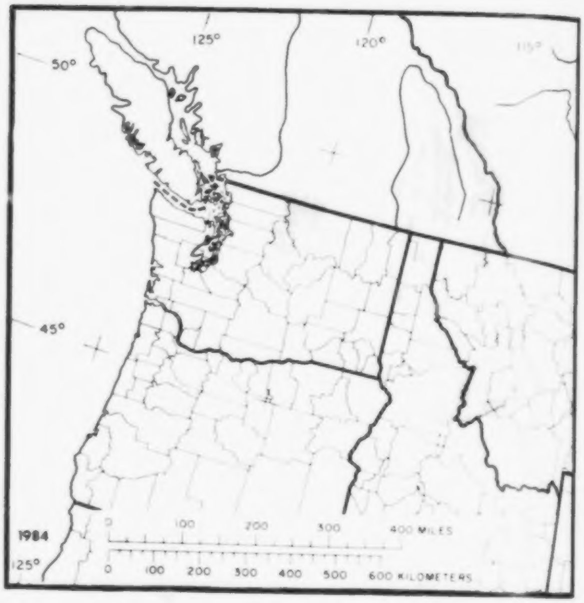

Figure 1—*The native range of alpine larch.*

Alpine larch (fig. 1) occupies a remote and rigorous environment, growing in and near the timberline on high mountains of the inland Pacific Northwest. Although alpine larch is found in both the Rocky Mountains and the Cascades, the two distributions are separated at their closest points by 200 km (125 mi) in southern British Columbia. This and smaller gaps in the species' distribution generally coincide with an absence of suitable high mountain habitat.

In the Rocky Mountains alpine larch extends from the Salmon River Mountains of central Idaho, latitude 45° 28′ N. northward to latitude 51° 36′ N. several kilometers past Lake Louise in Banff National Park, AB. [A fossil larch, probably of this species, grew between 1000 and 1250 A.D. near the Athabasca Glacier (Columbia Icefield) 90 km (56 mi) northwest of today's northernmost known isolated alpine larch tree *(18)*.] Within this distribution, alpine larch is common in the highest areas of the Bitterroot, Anaconda–Pintler, Whitefish, and Cabinet Ranges of western Montana. It is also found in lesser amounts atop numerous other ranges and peaks in western Montana and northern Idaho *(4)*. In British Columbia and Alberta, alpine larch is common along the Continental Divide and adjacent ranges, and in the Purcell and southern Selkirk Ranges.

In the Cascade Range alpine larch is found principally east of the Cascade Divide and extends from the Wenatchee Mountains (47° 25′ N.) in central Washington northward to about 21 km (13 mi) inside British Columbia (49° 12′ N.). Within this limited distribution covering a north-south distance of only 193 km (120 mi), alpine larch is locally abundant in the Wenatchee, Chelan, and Okanogan ranges.

Climate

Alpine larch grows in a very cold, snowy, and generally moist climate. The following description is based on weather records from several sites in and near alpine larch stands *(2)*. For more than half of the year, mean temperatures are below freezing. The cool "growing season," as defined by mean temperatures of more than 6° C (42° F) *(6)*, lasts about 90 days, and occasional frosts and snowfalls occur during the summer. July mean temperatures range from about 9° to 14° C (48° to 58° F). Long-term

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record low temperatures for late June through mid-August are near -5° C (23° F), whereas corresponding record highs are near 27° C (80° F). January mean temperatures range from about -14° C (7° F) in Alberta to -7° C (20° F) in the northern Cascades. Long-term record low temperatures have undoubtedly reached -50° C (-58° F) in some stands near the Continental Divide in Alberta and Montana.

Mean annual precipitation for most alpine larch sites is between 800 and 1900 mm (32 and 75 in), the larger amount being more prevalent near the crest of the Cascades. Most stands in the Montana Bitterroot Range evidently receive 1000 to 1500 mm (40 to 60 in). About 75 percent of this precipitation is snow and sleet.

Typically, the new snowpack begins to accumulate by late October. By mid-April, it reaches a maximum depth averaging about 2.1 m (7 ft) in stands near the Continental Divide and 3.0 to 3.5 m (10 to 11 ft) farther west. Maximum water content of the snowpack is attained in May and reaches about 75 cm (30 in) in stands near the Continental Divide and 100 to 125 cm (40 to 50 in) farther west. The snowpack does not melt away in most stands until early July. Average annual snowfall is probably about 1000 cm (400 in) in most stands west of the Continental Divide. Small amounts of stunted alpine larch grow on wind-exposed ridgetops and other microsites where snow accumulation is much less than the averages indicated above.

The inland Pacific Northwest often has a droughty period for a few weeks in late summer. This drought effect is minor in most alpine larch sites; however, dry surface soils may prevent seedling establishment in certain years. A modest quantity of rain falls through July and August, averaging 25 to 50 mm (1 to 2 in) per month in the United States, much of it associated with thunderstorms. In the Canadian Rockies summer precipitation is greater, 50 to 90 mm (2.0 to 3.5 in) per month, and more of it comes in Pacific frontal systems. Summertime relative humidity in alpine larch stands remains consistently higher than that recorded at lower elevations.

Most alpine larch stands annually experience winds reaching hurricane velocity, 117 km/h (73 mi/h) or more, during thunderstorms or during the passage of frontal systems. Ridgetop stands are exposed to violent winds most frequently.

Soils and Topography

Although soil development in alpine larch stands varies, most soils are immature. Generally alpine larch sites have undergone intense alpine glaciation during the Pleistocene and have been deglaciated for less than 12,000 years. Chemical weathering is retarded by the short, cool summer season. Also, nitrogen-fixing and other microbiotic activity that might enrich the soil is apparently restricted by low soil temperatures and high acidity.

Throughout its distribution, alpine larch commonly grows on slopes covered with granite or quartzite talus (boulders), which have not been previously occupied by vascular plants. The species also grows in cracks in massive bedrock. These undeveloped soils would probably be classified *(31)* as fragmental and as loamy skeletal families within the order Entisols *(Cryorthents)*. Such substrates have been referred to as azonal soils, and more specifically as Lithosols in earlier classifications.

On sites that have appreciable soil development or fine material (including recent moraines), the soils are still rocky and immature. These would be classified as Inceptisols—usually Typic Cryochrepts *(17)*.

On some sheltered slopes, deposits of volcanic ash in soil profiles are sufficiently thick to require recognition as Andic Cryochrepts, in a medial over loamy skeletal family *(15)*. Some of the best-developed ash-layered soils beneath alpine larch stands are Typic Cryandepts, which nearly fit the description of zonal Brown Podzolic soils in high elevation forests given by Nimlos *(19)*. These soils are strongly acidic and have a distinct, well-developed cambic B horizon.

Throughout the range of alpine larch, pH values were found to be very acidic, ranging from 3.9 to 5.7 in the mineral soil (B horizon) *(2)*. Bitterroot Range sites had an average pH of 4.6. Such strongly acid, shallow, rocky, and cold soils are extremely infertile.

Alpine larch grows on several types of geologic substrates but has an affinity for acidic rock types, being most abundant on granitic and quartzite substrates and absent or scarce on nearby limestone or dolomite *(4,21)*. This distribution contrasts markedly with that of several other cold-climate conifers, including Siberian larch *(L. sibirica)* and tamarack *(L. laricina)*, which often grow on basic, calcium-rich sites *(16,23)*.

Alpine larch achieves its best growth in high cirque basins and near the base of talus slopes where the soils are kept moist throughout the summer by aerated seep water (fig. 2). It can also tolerate boggy wet-meadow sites having very acidic organic soils. The species is most abundant on cool, north-facing slopes and high basins where it forms the uppermost band of forest (fig. 3). It also covers broad ridgetops and grows locally under relatively moist soil conditions on south-facing slopes. In the Canadian Rockies, where summer rainfall is more abundant, it is often found on south slopes. The extreme lower and upper altitudinal limits of subalpine larch, over its

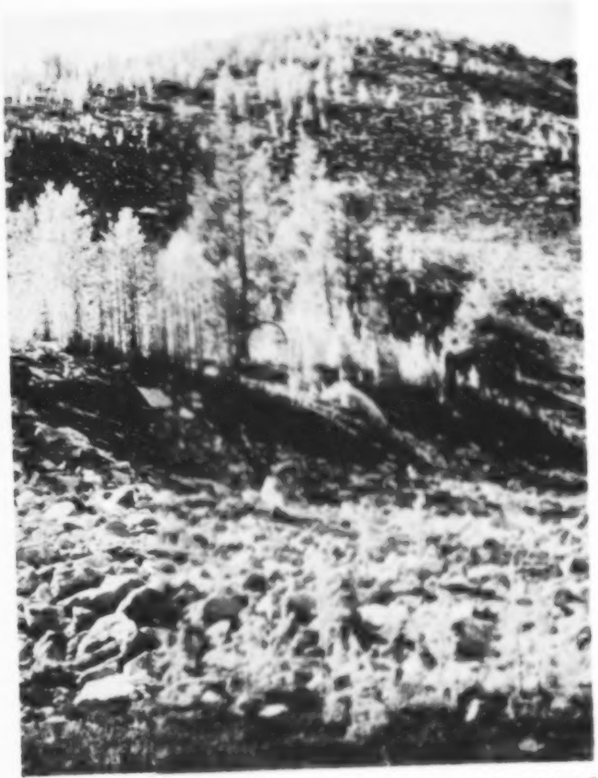

Figure 2—*Alpine larch on talus in a high basin, 2530 m (8,300 ft) elevation, on Lolo Peak, near Missoula, MT.*

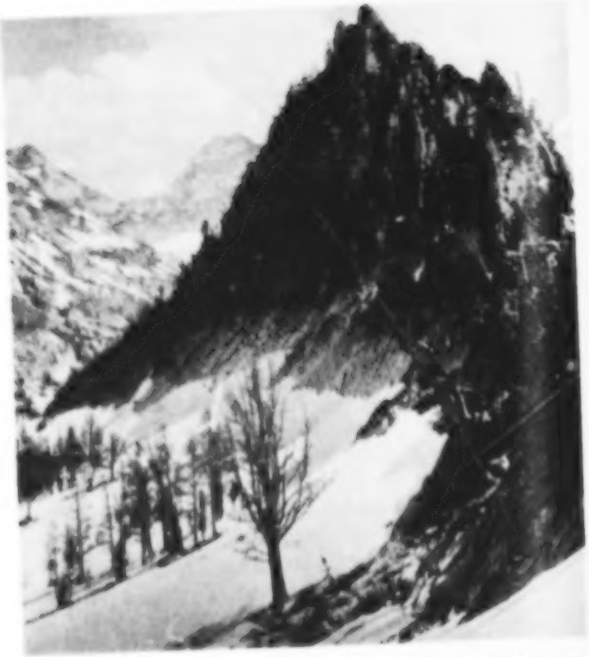

Figure 3—*Alpine larch on a snowy, rocky site at the base of a northfacing cliff.*

entire geographic range, are apparently 1520 and 3020 m (5,000 and 9,900 ft). The lowermost individuals are found in shady cirques and canyons in the North Cascades, while the highest limits apply to scattered stunted trees on Trapper Peak in the Montana Bitterroot Range *(2)*.

In the Bitterroot Range, alpine larch is abundant above 2290 m (7,500 ft) on northern exposures. It extends lowest on north-facing talus slopes, free from other competing conifers. But, even when moist, open, boulder-covered slopes extend down the mountainsides to the 1370 m (4,500 ft) canyon bottoms, alpine larch rarely colonizes them below 1980 m (6,500 ft).

In the Anaconda–Pintler Range of southwestern Montana, alpine larch forms a narrow band between elevations of about 2560 and 2800 m (8,400 to 9,200 ft). Northward in the Rockies, the elevation of its timberlines decreases gradually. Stands in northwestern Montana, Alberta, and southeastern British Columbia are generally found between 1980 and 2380 m (6,500 and 7,800 ft) and in the northern Cascades, between 1830 and 2290 m (6,000 and 7,500 ft).

Associated Forest Cover

Alpine larch grows in pure stands and also in association with whitebark pine *(Pinus albicaulis)*, subalpine fir *(Abies lasiocarpa)*, and Engelmann spruce *(Picea engelmannii)* near their upper limits. Alpine larch stands are primarily considered a variant forest cover type within Whitebark Pine (Society of American Foresters Type 208) *(26)*. The species is also associated with the upper elevations of Engelmann Spruce–Subalpine Fir (Type 206), especially in the Canadian Rockies. Near the crest of the Cascades, alpine larch is often associated with mountain hemlock *(Tsuga mertensiana)* and subalpine fir.

In Montana, stands above forest line (where subalpine fir is severely stunted) make up the *Larix lyallii–Abies lasiocarpa* habitat types classified by Pfister and others *(20)*. Alpine larch stands below forest line (in the subalpine fir zone) are classified generally as an edaphic (rock substrate) climax within the broader *Abies lasiocarpa/Luzula hitchcockii* habitat type, *Menziesia ferruginea* phase.

Four species dominate in the undergrowth of most alpine larch stands throughout the Pacific Northwest: grouse whortleberry (*Vaccinium scoparium*); smooth woodrush (*Luzula hitchcockii*); mountain arnica (*Arnica latifolia*); and red mountain heath (*Phyllodoce empetriformis*) *(2)*. But undergrowth beneath larch stands on bogs, recent moraines, alpine tundra, or rockpile sites, is distinctively different. Often shrublike (krummholz) subalpine fir and whitebark pine form an undergrowth layer beneath the larch on relatively cold or wind-exposed sites.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Alpine larch is monoecious; male and female flowers (strobili) are borne separately on short, woody spur shoots scattered among the leaf-bearing spur shoots. Strobili are normally monosporangiate. Buds producing the strobili begin to swell by the end of May, and the wind-dispersed pollen is shed from the small yellowish male strobili in June, when there is still several feet of snow on the ground in most stands *(2,21,30)*. Female strobili develop into purplish cones 4 to 5 cm (1.5 to 2.0 in) long by September. Frost damage, especially to female strobili, may account for low seed production in most years. The importance of other factors limiting pollination, fertilization, and seed development is unknown.

Seed Production and Dissemination—Large seed crops are infrequent. In Montana they occur about 1 year out of 10, and even modest-sized crops occur in about the same frequency. Appreciable quantities of seed are not produced until trees are at least 80 years old. Dominant trees, several hundred years of age, produce the largest crops.

Most of the relatively light, winged seeds fall from the cones in September and are wind disseminated *(30)*. Cleaned seeds number between 231 500 and 359 500/kg (105,000 and 163,000/lb).

A heavy seed crop in one area of the Washington Cascades was largely consumed by larvae of an unidentified fly (Diptera) *(2)*.

Seedling Development—Germination of alpine larch seed has been poor in several tests but is improved by soaking the seeds for 24 hours in 3 percent hydrogen peroxide solution *(8,21,24,30)*. Such treatment may inhibit root development, however *(25)*. There are usually five cotyledons, although four or six may appear; they are narrow, pointed, and 1.0 to 1.5 cm (0.4 to 0.6 in) long. Germination is epigeal.

First-year germinants of alpine larch are seldom found in natural stands. In one area the smallest seedlings observed were 4 cm (1.6 in) high and proved to be about 10 years old *(4)*. Several cotyledon-stage seedlings were found on an Alberta site in 1977 following a good seed year *(21)*.

Small openings in cirques often contain dense, even-aged groves, termed "reproduction glades," of alpine larch seedlings or saplings. This suggests that successful reproduction occurs rarely, and only under ideal conditions. The location of reproduction glades suggests that germination is most successful on a moist mineral soil surface, on northern exposures or in cirques not fully exposed to afternoon sun. Germination probably takes place in July soon after snowmelt.

Seedlings and basal branches of saplings have juvenile leaves that last through two summers. Until the plants are 20 to 25 years old, this evergreen, or "wintergreen," foliage constitutes 25 to 30 percent of the total leaf biomass *(21,22)*. Physiological studies suggest that this wintergreen foliage is important for tree establishment because it is less susceptible to drought stress in summer.

Height growth is exceedingly slow for the first 20 to 25 years but accelerates rapidly thereafter *(21,22)*. This pattern of early growth apparently allows the seedlings to become well established and develop an extensive root system while still being protected from winter and spring desiccation by the snowpack.

This species is very difficult to cultivate even in the relatively cool climates at lower elevations in the Pacific Northwest or in England. Seedlings have been raised at Kew Gardens *(12)*, but they have not grown well, leading to the conclusion that a colder climate than that of Britain is required for alpine larch. Apparently, daytime high temperatures and surface drought are lethal. The species seems to require full light, but low temperatures. Bud dormancy is thought to influence the lack of adaptation to lower elevations *(17)*.

Vegetative Reproduction—Subalpine larch does not reproduce from sprouts. Techniques for reproduction from rooted cuttings have not been reported. Layering (rooting of lower branches that are compressed against moist ground) has long been known in some other species of *Larix* *(11)* and in its associate, subalpine fir, but alpine larch is known to spread by layering only in a few severely stunted trees or krummholz *(4)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Alpine larch is a very slow-growing, long-lived tree. Vigorous saplings 1.2 m (4 ft) tall are about 30 to 35 years of age. Dominant trees attain small to moderate dimensions, depending upon site conditions, in a typical 400- to 500-year life span. Average ages for dominant alpine larch of different diameters are as follows *(2)*:

D.b.h.		Total age	
		Average site	Very good site
cm	*in*	*years*	
13	5	150	75
25	10	250	125
38	15	350	175
51	20	500	225
99	39	—	450

The largest diameter shown is not attained on "average" sites.

Although from four to five centuries is a common life span for dominant trees, many individuals attain 700 years, and the oldest are estimated to be about 1,000 years *(2)*. Complete ring counts are not possible on the oldest trees because of extensive heart rot. On average sites (high on north-facing slopes) the dominant trees grow 12 to 15 m (40 to 50 ft) in height and 30 to 61 cm (12 to 24 in) in d.b.h. In moist cirque basin sites on granitic or quartzite substrates, dominant trees reach 23 to 29 m (75 to 95 ft) in height and 61 to 124 cm (24 to 49 in) in d.b.h. The largest recorded alpine larch, in the Wenatchee National Forest of Washington State, is 201 cm (79 in) in d.b.h. and 29 m (95 ft) tall *(1)*. The tallest reported alpine larch is an exceptional 46 m (152 ft) in Montana's Cabinet Range *(3)*.

Alpine larch (fig. 4) typically grows in open, parklike groves, less than 0.2 ha (0.5 acre) in size, interspersed with natural openings of various sizes. Stocking within the small groves is at the rate of 125 to 200 mature trees per hectare (50 to 80/acre) *(2)*.

No site index or yield data have been developed for alpine larch stands; however, data from other Montana forest habitat types *(20)* suggest that annual yield capability would be only about 0.7 to 1.4 m^3/ha (10 to 20 ft^3/acre) on sites having better than average productivity. Defect is very high for all species in alpine larch communities. Essentially no commercial timber harvesting has been done, even in the best developed stands, nor does any seem likely in the future.

"Poor" alpine larch sites produce stunted larch generally 5 to 11 m (16 to 36 ft) tall at maturity. Many of these sites lie above the tree line for evergreen conifers and would be classified as alpine tundra were it not for the occurrence of this unusual tree.

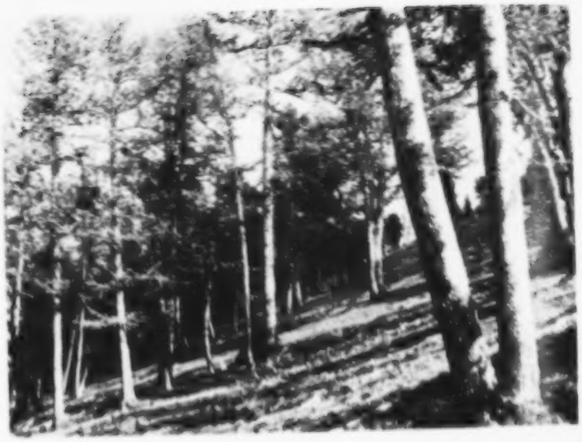

Figure 4—*Mature alpine larch in Deerlodge National Forest, MT.*

Rooting Habit—Alpine larch roots extend deep into fissures in the rocky substrate. Trees are well anchored by a large taproot and large lateral roots and are very windfirm. The crown and trunk of old trees may break off in violent winds, but the tree itself is seldom uprooted.

Richards *(21)* found that subalpine larch "seedlings" 16 to 25 years old and only 20 to 40 cm (8 to 16 in) tall had taproots penetrating 40 to 60 cm (16 to 24 in) and laterals descending 20 to 60 cm (8 to 24 in) at about 45° from the horizontal. Mycorrhizal development was found on all trees, but shallow roots had a higher degree of mycorrhizal association than deep roots. *Cenococum graniforme* has been identified as an ectotrophic mycorrhiza of subalpine larch *(29)*.

Reaction to Competition—Alpine larch is the most shade-intolerant conifer growing at these high elevation sites and is classed as very intolerant. Its evergreen associates attain their best development in forests below the lower limits of larch. An exception is whitebark pine, another timberline inhabitant, which, however, is most abundant on warm exposures and microsites and thus tends to complement rather than compete with larch *(4)*. Alpine larch foliage requires higher light intensities than its evergreen associates to maintain active growth through photosynthesis *(21,22)*. Thus it is unable to compete with a *vigorous* growth of evergreens. Instead, alpine larch owes its existence to its superior hardiness, especially on cool exposures. At the highest elevations alpine larch fills a vacant niche and represents the potential climax. The larch's ability to grow at higher elevations than evergreen conifers on certain sites is partly related to its superior resistance to winter desiccation—dehydration of foliage during warm, sunny periods when the roots are still frozen or chilled *(21,22)*. Winter desiccation in conjunction with lack of summer warmth are thought to be primary factors limiting the ascent of tree growth on high mountains *(5,28)*. Above the limit of trees, the growing season is so short that new growth cannot adequately harden-off (fully developed cuticle), and thus it succumbs to desiccation in winter.

Alpine larch is less vulnerable to winter desiccation than its associated conifers because its leaves are deciduous and its buds are woody and protected *(2,21)*. Thus there is little tendency for larch to grow in a shrubby or krummholz form, unlike its evergreen associates. Its deciduous foliage requires a large amount of moisture throughout the summer compared to the evergreens; consequently, it occupies relatively moist sites.

In the middle of its zone of occurrence [between "forest line," the general upper limit of contiguous forest, and "tree line," the general limit of erect evergreen conifers *(5)*], natural openings and severe climate allow alpine larch to share climax status with subalpine fir, Engelmann spruce, and whitebark pine. These evergreens often develop in the shelter of a large "patriarch" larch, sometimes growing up through the larch crown as if it were a trellis.

On the better sites where alpine larch grows, subalpine fir is the potential climax dominant. Engelmann spruce is usually a minor component of stands containing subalpine larch; it often attains large size but, unlike subalpine fir, seldom regenerates abundantly.

Occasionally alpine larch seeds in and regenerates on a burned area within the subalpine forest, 100 to 150 m (330 to 490 ft) below its usual elevational limits. But the species grows more slowly than the accompanying lodgepole pine (*Pinus contorta* var. *latifolia*) and is crowded out by that species and by subalpine fir and Engelmann spruce.

Damaging Agents—Violent winds in alpine larch stands often damage crowns in conjunction with loads of clinging ice or wet snow. Nevertheless this tree's deciduous habit and supple limbs make it more resistant to wind damage than its associates. Death usually occurs when advanced heart rot has so weakened the bole that high winds break off the trunk. The quinine fungus *(Fomitopsis officinalis)*, which causes brown trunk rot, produces the only conks commonly found on living trunks. This fungus is evidently the source of most heart rot.

Other diseases and insects generally cause little damage to alpine larch. Needle blight fungi, *Sarcotrochila alpina*, has severely infected trees on Mount Frosty in Manning Provincial Park, BC *(33)*. Needle cast fungi, *Lophodermium laricinum*, have also been reported on alpine larch. Alpine larch is listed as a host of two fungi, *Lachnellula occidentalis* and *L. suecica (13)*, which may be capable of causing stem cankers, but neither has been noted as a serious disease problem.

Isolated witches'-brooms (dense branch-clusters with associated branch swelling) are found widely scattered in alpine larch stands. These could be caused by dwarf mistletoe, fungal infection, or perhaps even genetic aberration. The western larch dwarf mistletoe *Arceuthobium laricis* was reported in two early 1900's collections on alpine larch, but its status on this species is poorly known *(14)*.

Snow avalanches and snowslides are an important source of damage in many stands, but again this species is better adapted to survive these disturbances than its evergreen associates. Alpine larch poles up to 13 cm (5 in) thick and 6 m (20 ft) tall can survive annual flattening by snowslides only to straighten again when the snow melts in summer *(4)*. As larch poles exceed this size their strong trunks and lack of dense foliage make them resistant to breakage in snowslides. Because of this superior resistance, alpine larch often occupies snowslide sites (forming a "disclimax" because of disturbance) within the subalpine forest proper.

Fire is an occasional but quite localized cause of injury or death in alpine larch stands. Large fires are infrequent in these cool, moist, and rocky sites where fire spreads poorly because of the light and discontinuous fuels. Unlike its thick-barked, fire resistant relative, western larch *(Larix occidentalis)*, alpine larch has thin bark and has low resistance to surface fire.

Special Uses

Alpine larch's primary values seem to be in watershed protection, wildlife habitat, and outdoor recreation and esthetics. The ability of this larch to occupy steep north slopes and snow chutes where other trees scarcely grow suggests that it helps to stabilize snow loads and reduce the severity of avalanches *(27)*. Scientists from several countries (Switzerland, Iceland, Japan, and New Zealand) who are interested in avalanche control or forest establishment on cold sites have obtained alpine larch seed from the USDA Forest Service.

A diverse assemblage of birds and mammals is associated with alpine larch communities *(2)*. Grizzly bears often dig winter dens in alpine larch stands in Banff National Park *(32)*. The greatest use of these habitats by most wildlife species is as summer range, when timberline vegetation is succulent, temperatures cool, and water abundant. Mountain goats, bighorn sheep, hoary marmots, pikas, mule deer, elk (wapiti), black and grizzly bears, red squirrels, and snowshoe hares are among the mammals that feed in alpine larch stands. Blue grouse apparently feed heavily on alpine larch needles. The trees provide some concealment and thermal cover in an otherwise open habitat. Woodpeckers and other cavity-nesting birds and mammals nest in the larger, hollow-trunk trees.

Hikers and photographers are attracted by the natural beauty of alpine larch stands. The tree's foliage is a translucent bright green in summer and turns lemon yellow and finally golden in September before it falls in October.

The unusual hardiness of this species, its adaptations to survival in a harsh climate, on rugged topography and sterile substrates, should make it of special interest for scientific study and for reclamation plantings on high-elevation sites.

Genetics

Races, varieties, or subspecies of alpine larch are not known. The species' restricted environmental tolerances and geographical and altitudinal distributions may have limited the opportunity for development of genetic variation.

Apparent natural hybridization of alpine larch and western larch has been documented in western Montana *(8,9,10)*. Although these species occupy a similar geographic area, they inhabit different altitudinal zones and are usually separated from each other by 150 to 300 m (500 to 1,000 ft) of elevation at their closest proximities. Nevertheless, their distributions occasionally overlap slightly in north-slope snowslide chutes or talus rockpiles. Apparent natural hybrids have been identified in two overlap areas using a hybrid-index formula. The two species were also artificially cross-pollinated and the resulting seed and that from control species was planted. Distinct morphological differences were noted among the two species and the putative hybrid. The two species also vary in external and internal characteristics even when they grow side by side, confirming their genetic difference *(8,9)*.

An interesting mixture of both larch species and various intermediate (hybrid) forms occurs on a rocky site in the Carlton Ridge Research Natural Area in the Lolo National Forest south of Missoula, MT *(10)*.

The chromosome complement of subalpine larch is 2N=24, similar to that of most other trees in the pine family *(Pinaceae) (7)*.

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Larix occidentalis Nutt. Western Larch

Pinaceae Pine Family

Wyman C. Schmidt and Raymond C. Shearer

Western larch *(Larix occidentalis)*, a deciduous conifer, is also called tamarack and western tamarack; less commonly used names are hackmatack, mountain larch, and Montana larch *(17)*. It is largest of the larches and is the most important timber species of the genus. Western larch is used for lumber, fine veneer, poles, ties, mine timbers, and pulpwood.

Habitat

Native Range

Western larch (fig. 1) grows in the Upper Columbia River Basin of northwestern Montana, northern and west central Idaho, northeastern Washington, and southeastern British Columbia; along the east slopes of the Cascade Mountains in Washington and north-central Oregon; and in the Blue and Wallowa Mountains of southeastern Washington and northeastern Oregon.

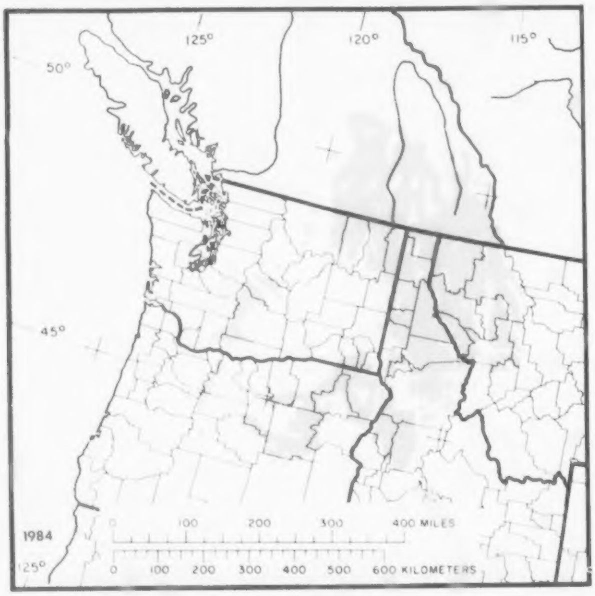

Figure 1—*The native range of western larch.*

Climate

Western larch grows in a relatively moist-cool climatic zone, with low temperature limiting its upper elevational range and deficient moisture its lower extremes *(44)*. Mean annual temperature within the larch zone is about 7° C (45° F), but annual maximums average 29° C (84° F) and minimums average -9° C (15° F) (table 1) *(35)*. Average temperatures during the May through August growing season are about 16° C (60° F) with July the warmest month. The frost-free season varies from about 60 to 160 days, usually from early June through early September. Frosts can occur any month of the year.

Annual precipitation in larch forests averages about 710 mm (28 in) in the north part of its range to 810 mm (32 in) in the south. The extremes where larch grows are about 460 mm (18 in) and 1270 mm (50 in). About one-fifth of the annual precipitation occurs during the May through August growing season, most of it in May and June. July and August are usually dry and are characterized by clear, sunny days (60 to 80 percent of the daylight hours), low humidity, and high evaporation rates *(44)*. Elevation and geographic location affect both the amount and the form of precipitation. On midelevation sites, snow commonly blankets most larch forests from November to late April and accounts for over half the total precipitation. Snow accounts for an even higher proportion of the total precipitation in the northerly

Table 1—Summary of weather data from within the range of western larch[1]

	C	*F*
Average temperature		
Annual maximum	29	84
Annual minimum	-9	15
Annual mean	7	45
Annual absolute maximum	41	106
Annual absolute minimum	-37	-34
Growing season only	15	59
	mm	*in*
Average precipitation		
Total annual	710	28
Total during growing season[2]	160	6
Total snowfall	2620	103

[1] Data compiled from 12 weather stations in Idaho, 10 in Montana, 3 in Oregon, and 4 in Washington using U.S. Department of Commerce summaries for 1951 through 1960 (35).
[2] May through August.

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higher elevation portions of larch forests. One high elevation larch site at Roland, ID, receives an average of 620 cm (244 in) of snow annually. Lower elevation sites commonly receive an average of more than 150 cm (60 in) of snow.

Soils and Topography

Western larch grows on a wide variety of soils. The most extensive soils have developed in glacial till or colluvium composed of materials derived from limestone, argillite, and quartzite bedrocks of the Precambrian belt geologic series. Larch also grows on soils developed in Recent and Tertiary alluvium and Pleistocene lake sediments. Most soils suitable for the growth of western larch are deep and well drained. Soils developed in glacial till, colluvium, and recent alluvium have nongravelly to gravelly loamy surfaces and gravelly to extremely gravelly loamy subsoils. Volcanic ash is often incorporated into the surface horizon. Soils developed in Tertiary sediments or Pleistocene lake sediments have silt loam surfaces and silt loam, silty clay loam, silty clay, or clay subsoils.

Most soils supporting the growth of western larch are classified in two orders of the soil taxonomy: Inceptisols and Alfisols. Occasionally western larch is found on soils of the order Spodosols, but Spodosols are not extensive within the range of western larch and generally occur above the upper elevational limits of the species. A majority of the soils supporting the growth of western larch are the Cryoboralf, Cryochrept, and Cryandept great groups. Mean annual soil temperature of the soils within the great groups is about 5° C (41° F) at 51 cm (20 in). At low elevations on southern or western exposures within the range of western larch, soil temperatures are warmer and soils supporting the growth of western larch are in the Eutroboralf and Eutrochrept great soil groups.

Western larch grows best on the more moist Eutrochrepts or Eutroboralfs and the lower elevation (warmer) Cryochrepts and Cryoboralfs. It is commonly found growing on valley bottoms, benches, and north- and east-facing mountain slopes. South and west exposures are often too severe for larch seedling establishment, particularly on the drier sites found at larch's lower elevational limits and the southern portion of its range. On moist sites found in the mid- to northern-portion of its range and on mid- to high-elevation sites, larch grows on all exposures.

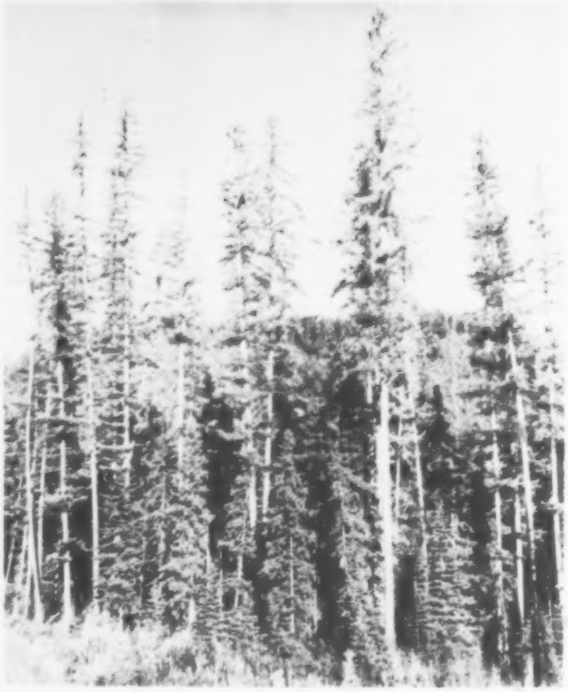

Figure 2—*A mature stand of western larch with an understory of the more tolerant Engelmann spruce and subalpine fir.*

Associated Forest Cover

Western larch (fig. 2) is a long-lived seral species that always grows with other tree species. Young stands sometimes appear to be pure, but other species are in the understory. Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) is its most common tree associate. Other common tree associates include: ponderosa pine (*Pinus ponderosa*) on the lower, drier sites; grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and western white pine (*Pinus monticola*) on moist sites; and Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and mountain hemlock (*Tsuga mertensiana*) in the cool-moist subalpine forests (*44*).

Western larch makes up a majority or plurality in the forest cover type Western Larch (Society of American Foresters Type 212) (*43*). It is included in 11 other cover types:

205 Mountain Hemlock
206 Engelmann Spruce–Subalpine Fir
210 Interior Douglas-Fir

213	Grand Fir
215	Western White Pine
218	Lodgepole Pine
220	Rocky Mountain Juniper
224	Western Hemlock
227	Western Redcedar–Western Hemlock
228	Western Redcedar
237	Interior Ponderosa Pine

Classification systems based on potential natural vegetation have been developed for much of the geographic area where western larch grows. Larch is a seral species in 13 of the 21 habitat types described for eastern Washington and northern Idaho *(7)*. In Montana, larch is a significant component in 20 of the 64 forest habitat types *(21)*. Of these 20 habitat types, larch is a major seral species in 12, and a minor seral species in 8. These habitat types are found within the following forest series: the relatively dry-warm Douglas-fir; the moist grand fir, western redcedar, and western hemlock; and the cold-moist subalpine fir.

Larch forests typically have a rich understory flora with dense herbaceous and less dense shrub layers. It is not unusual to find as many as 7 tree species and 40 undergrowth species in plots of 405 m^2 (4,356 ft^2) *(21)*. On a 40-ha (100-acre) study area on the Coram Experimental Forest in northwestern Montana, 10 conifer, 21 shrub, and 58 herbaceous species were recorded *(31)*. Some of the common understory species associated with larch are the following:

Shrubs

Rocky Mountain maple	*Acer glabrum*
Sitka alder	*Alnus sinuata*
Serviceberry	*Amelanchier alnifolia*
Oregongrape	*Berberis repens*
Menziesia	*Menziesia ferruginea*
Mountain lover	*Pachistima myrsinites*
Ninebark	*Physocarpus malvaceus*
Rose	*Rosa* spp.
Thimbleberry	*Rubus parviflorus*
Common snowberry	*Symphoricarpos albus*
Dwarf huckleberry	*Vaccinium caespitosum*
Blue huckleberry	*Vaccinium globulare*
Scouler willow	*Salix scouleriana*
Spiraea	*Spiraea betulfolia*

Herbs

Wild sarsaparilla	*Aralia nudicaulis*
Kinnikinnick	*Arctostaphylos uva-ursi*
Arnica	*Arnica latifolia*
Pinegrass	*Calamagrostis rubescens*
Queenscup	*Clintonia uniflora*
Fireweed	*Epilobium angustifolium*
Twinflower	*Linnaea borealis*
Beargrass	*Xerophyllum tenax*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Western larch is monoecious; both staminate and ovulate flowers develop throughout the crown. Buds are found at the end of short spurlike lateral branchlets. Vegetative buds are smaller than flower buds—usually about 2.5 to 3.0 mm (0.10 to 0.12 in) in diameter, whereas flower buds range from about 3.0 to 4.8 mm (0.12 to 0.19 in) in diameter. Ovulate buds are one to one and one-half times longer than they are wide and are rounded or conical on the end. Staminate buds are usually globose and about one and one-half to two times longer than wide. Vegetative and flower buds can be detected early in the fall, about 1 year before subsequent cone crops mature. Methods of sampling buds and conelets have been devised for forecasting larch seed crops on individual trees, as well as stands *(24)*.

Pollen and seed conelets appear several days before vegetative buds open—usually from about April 15 to May 15 *(44)*. Conelets are generally very conspicuous, varying from bright red to green. Pollination occurs in late May and early June *(33)*. Cones complete their development in one season and mature by mid- to late-August, reaching 2.5 to 4.5 cm (1.0 to 1.8 in) in length.

Cones usually begin to open by early September, but in cool-moist summers cone opening may be delayed a month or longer. More than 80 percent of the seeds usually are dispersed by mid-October *(44)*. Cones open when they have dried to a moisture content of 35 to 40 percent, opening at the same time on individual trees, but varying substantially among trees in the same stand *(39)*. Cones usually fall from the tree during the following winter, but many may stay attached through the next summer.

Seed Production and Dissemination—Larch is a good seed producer, but cone crops vary substantially by year and location. Long-term records of larch seed production in Montana show that good seed crops are produced at about 5-year intervals with fair to poor crops in the intervening years *(44)*. Two good crops or several poor crops, however, may occur in close succession. Overall, the ratio of good or fair to poor seed crops is about 1 to 1.

Cone production is infrequent on larch trees less than 25 years old, although trees as young as 8 years occasionally produce cones. Larch starts bearing abundant cone crops from 40 to 50 years and continues bearing heavily for 300 to 500 years *(35)*. Only dominants and codominants produce significant numbers of cones *(44)*.

Cone production usually is a function of crown size because larch bears cones throughout the crown. Trees with the largest crowns produce the most cones. During a good cone year, production ranged from a low of 56 cones in one tree with 45 major branches to a high of 2,090 cones in another tree with 95 major branches. Also, vigorous, full-crowned, mature trees averaging 56 cm (22 in) in diameter produced about five times as many seeds as 36-cm (14-in) trees in the same stand and age class *(44)*.

A mature cone may have as many as 80 filled seeds per cone, but the average is about half that number *(39)*. Seed viability is related to cone-crop size, ranging from a low of 5 to 10 percent viability in poor crops to 70 to 80 percent in good crops. Young trees usually produce seeds of higher viability than overmature trees.

Larch seeds are small and lightweight, averaging 302,000/kg (137,000/lb) *(45)*. Because of their relatively large wing, they are dispersed to greater distances than the heavier seeds of Douglas-fir and subalpine fir, but to about the same distance as the light seed of Engelmann spruce *(37)*. Larch seed may be dispersed 240 m (787 ft) from clearcut boundaries under normal wind conditions (fig. 3). Although the seeds traveling that distance are only about 5 percent of that falling within the timber, they may amount to 100,000/ha (40,000/acre) in a heavy seed year—more than is adequate to restock favorable seedbeds. Overstocking often occurs near the seed source when bare soil is exposed. Seeds are disseminated more uniformly in seed tree and shelterwood cuttings than in clearcuts.

Seed production in mature natural stands of larch may exceed 1.2 million seeds per hectare (0.5 million seeds/acre) in a heavy seed crop. Records at Coram Experimental Forest indicate that small rodents eat only about 1 to 3 percent of the seeds during the overwintering period *(41)*. In contrast, rodents usually feed heavily on the larger seeds of Douglas-fir and ponderosa pine during this same period.

Larch seed germinates about the time of snowmelt, from late April to early June, usually 1 to 2 weeks before associated tree species *(38)*. Germination is epigeal *(45)*. Natural stratification of larch seeds during the winter prompts rapid and complete germination. Without stratification, spring-sown larch seeds germinate slowly and erratically, with some seeds holding over until the next season. Artificial stratification methods using cold-moist conditions work well for preparing seed for field germination. These same seed treatments, as well as those using stimulants, such as hydrogen peroxide, are particularly useful for testing germinative energy and capacity *(26)*. Air temperatures of about 27° C (80° F) are ideal for larch seed germination, but seeds germinate at temperatures 10° to 15° C (17° to 27° F) cooler than that.

Seedling Development—Western larch is a seral species well adapted to seedbeds exposed by burning *(9)* or mechanical scarification *(35,40)*. Seedbeds of undisturbed litter, humus, sod, and areas with heavy root competition are poor for larch seedling survival.

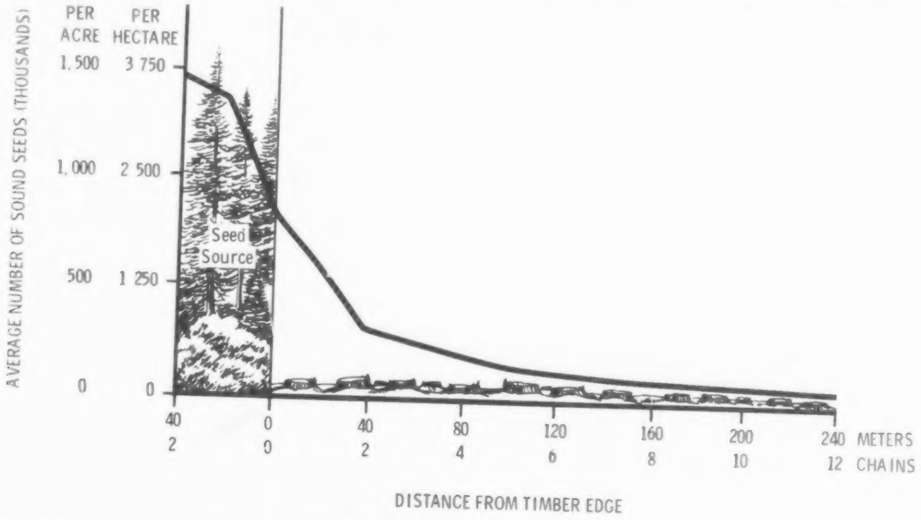

Figure 3—*Dispersal characteristics of sound western larch seed from a seed source along a clearcut boundary.*

Most seedling losses occur the first growing season—after 3 years seedling losses are minor *(35)*. For example, studies on areas favorable for larch show that 54 percent of the seedlings survived the first season; 85 percent of the remaining seedlings survived the second season; and by the fifth season the remaining seedlings' survival was 94 percent. In other studies, an average of 39 percent of the larch seedlings survived the first 3 years *(44)*.

Seedling survival is affected mostly by biotic factors early in the growing season and by physical factors late in the season. Until about mid-July mortality is caused primarily by fungi, rodents, birds, and insects. Most losses of first-year seedlings, particularly those growing on duff, are caused by fungi, usually immediately after germination. Seedlings growing on mineral soil seedbeds are far less susceptible to fungi than their counterparts growing on duff under both full sun and partial shade. Under full shade, however, susceptibility on the two types of seedbed is reversed *(44)*. Seedling losses to animals, insects, and birds are relatively minor overall but may be heavy in specific locations and years.

Insolation is the most important physical factor affecting larch seedling survival *(38)*. High soil surface temperatures exceeding 57° C (135° F) are not uncommon starting in late June, resulting in heat girdling of seedlings at the soil-air interface. Again, duff is the least desirable seedbed, with lethal temperatures occurring earlier in the season and on more days. Lethal soil temperatures are reached most frequently on duff, less on burned mineral soil, and least on scarified mineral soil. On south and west slopes, soil surface temperatures exceed 79° C (175° F), and few larch seedlings survive regardless of the type of seedbed *(38)*.

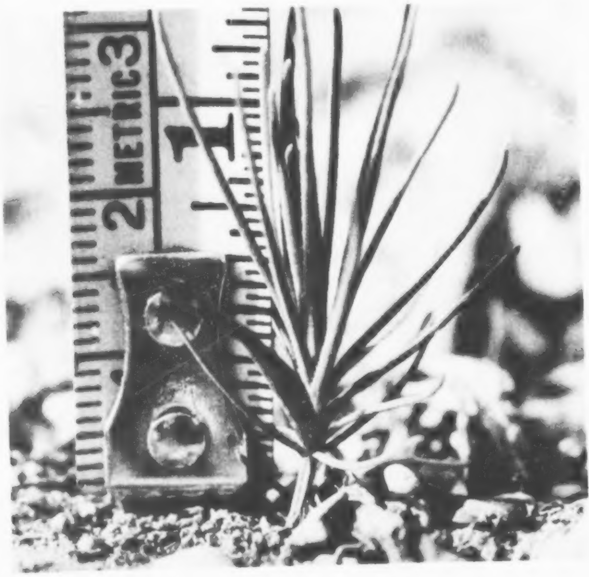

Figure 4—*Newly germinated seedlings of larch are usually robust and rapidly develop a vigorous root system.*

Drought is the major physical factor affecting mid- to late-season seedling survival. Unlike insolation, drought losses are heaviest in full shade because of the heavy competition for moisture by all the associated tree and understory vegetation.

Although aspect affects germination very little, it has a pronounced effect on seedling survival. North, northwest, and northeast exposures and gentle to flat topography provide the most favorable conditions for larch seedling survival. High surface temperatures and droughty conditions on the south and west exposures preclude survival of any significant number of larch seedlings. As a result, larch is either absent or but a minor stand component on hot, dry slopes.

Larch seedlings grow about 5 cm (2 in) the first growing season (fig. 4). In shade, root penetration may average only 2.5 cm (1 in) the first year, while its counterparts growing in the sun or partial shade may have 23 cm (9 in) roots. Seedlings growing in partial shade usually grow faster in height than seedlings in full sunlight for the first few years, but faster in full sunlight after that.

Larch seedlings break dormancy very easily. Buds usually burst by late April, well before those of any other native conifers. Shoot growth starts from late May to mid-June.

Larch seedlings grow rapidly in spite of the relatively short growing season of the Northern Rockies. Average annual height growth of about 30 cm (12 in) for the first 4 years is common *(44)*. Of its major associates only lodgepole pine matches the rapid juvenile height growth of western larch. Douglas-fir seedlings grow at about one-half the rate of larch, and Engelmann spruce and subalpine fir seedlings grow at about one-fourth the rate of larch *(28)*.

Vegetative Reproduction—Larch does not reproduce by sprouts. Cuttings have been successfully rooted by researchers at the Intermountain Forest and Range Experiment Station, but methods have not been fully tested at this time. One technique requires cutting 8 to 10 cm (3 to 4 in) scions from young larch trees, dipping the lower portion of the cutting in a powder mixture of 0.8 percent indolebutyric acid and 10.0 percent Captan 50 wettable powder (mixed with talc), and placing them in a rooting chamber at about 24° C (75° F). Researchers

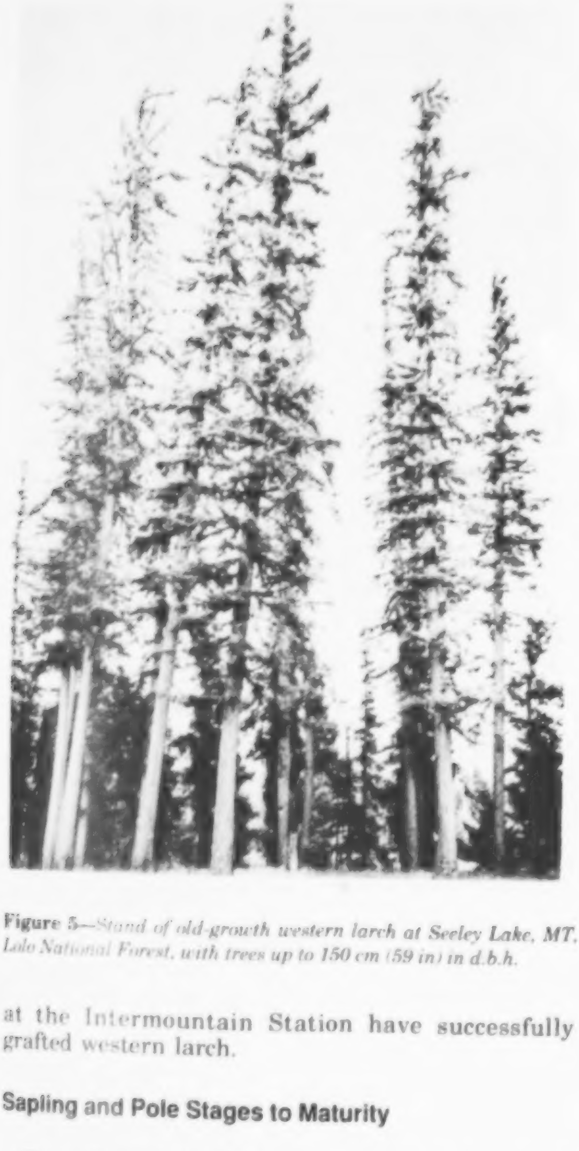

Figure 5—*Stand of old-growth western larch at Seeley Lake, MT, Lolo National Forest, with trees up to 150 cm (59 in) in d.b.h.*

at the Intermountain Station have successfully grafted western larch.

Sapling and Pole Stages to Maturity

Growth and Yield—Western larch is long-lived and is the largest of the world larches *(20)* (fig. 5). Trees exceeding 230 cm (90 in) d.b.h. and 900 years of age have been found *(44)*. Larch normally reaches 30 to 55 m (100 to 180 ft) in height at maturity and occasionally exceeds 61 m (200 ft).

Table 2—Height of average dominant and codominant western larch by age and site index

	Site index at base age 50 years		
Age	**12.2 m or 40 ft**	**18.3 m or 60 ft**	**24.4 m or 80 ft**
yr	*m*	*m*	*m*
20	3	4	6
40	9	14	19
60	14	21	29
80	17	26	35
100	20	30	40
yr	*ft*	*ft*	*ft*
20	9	14	19
40	31	47	63
60	47	70	94
80	57	86	115
100	65	97	130

Table 3—Average site indices for larch *(21,35)*

Ecological habitat type	Average site index at base age 50 years	
	m	*ft*
Northern Idaho and Washington:[1]		
Abies lasiocarpa-Xerophyllum tenax	14.9	49
Abies lasiocarpa-Pachistima myrsinites	17.7	58
Tsuga heterophylla-Pachistima myrsinites; Thuja plicata-Pachistima myrsinites; Abies grandis-Pachistima myrsinites	20.1	66
Pseudotsuga menziesii-Physocarpus malvaceus	18.9	62
Pseudotsuga menziesii-Calamagrostis rubescens	16.8	55
Montana:		
Pseudotsuga menziesii-Vaccinium caespitosum	18.0	59
Pseudotsuga menziesii-Physocarpus malvaceus	17.4	57
Pseudotsuga menziesii-Linnaea borealis	16.8	55
Picea-Vaccinium caespitosum	22.6	74
Thuja plicata-Clintonia uniflora	19.2	63
Tsuga heterophylla-Clintonia uniflora	24.4	80
Abies lasiocarpa-Clintonia uniflora	19.2	63
Abies lasiocarpa-Linnaea borealis	17.1	56
Abies lasiocarpa-Menziesia ferruginea	20.4	67
Abies lasiocarpa-Xerophyllum tenax	15.5	51

[1] Based on Daubenmire's classification *(6)*

Larch grows faster in height than any other conifer in the Northern Rockies for the first century, giving this highly shade-intolerant species the height advantage it needs to survive. For the first 50 years, larch and lodgepole pine height growth are similar, but thereafter lodgepole height growth declines in comparison with larch.

Differences in height growth of larch and its associated species are readily apparent at early ages. Both larch and lodgepole pine start off faster than their associates. Studies on good quality sites on Coram Experimental Forest in Montana show larch and lodgepole pine growing at about twice the rate of Douglas-fir and three to four times faster than subalpine fir and Engelmann spruce for the first 20 years. On wetter sites in northern Idaho, larch and lodgepole pine typically grow much faster than western white pine, western hemlock, and western redcedar in unthinned natural stands for the first half century. In thinned stands, however, differences in height growth of western white pine and larch are nominal. By age 100, the height growth advantage larch holds over its associates typically becomes less pronounced *(35,10)*.

Site productivity accounts for the largest share of the variation in height growth of larch throughout its range. Site index curves for larch (base age of 50) show heights at age 100 ranging from 20 m (65 ft) on low sites to 40 m (130 ft) on high sites (table 2). Average site indices for larch on different ecological habitat types are given in table 3.

Physiographic position, directly interrelated with habitat type, also influences height growth. Larch grows most rapidly in height on the deep, moist soils of valley bottoms and lower north and east slopes, but poorly on the upper south and upper west slopes *(35)*:

Physiographic class	Average site index	
	m	*ft*
Valley bottoms	18.9	62
Midnorth and mideast facing slopes, lower south and lower west facing slopes and benches	18.0	59
Upper north and upper east facing slopes	17.4	57
Midsouth and midwest facing slopes	16.2	53
Upper south and upper west facing slopes	13.4	44

Seedbed conditions at the time of seedling establishment influence height growth in the formative years *(27)*. Studies on Priest River Experimental Forest in northern Idaho showed that on the average 2-year-old larch seedlings were twice as tall on burned seedbeds as they were on bare mineral or duff-covered soil *(14)*. Subsequent studies on Coram Experimental Forest showed that these height growth differences persisted into the teenage years, with larch growing about one-third faster on burned seedbeds than on scarified or undisturbed seedbeds *(35)*. These differences may be due to changes in nutrient availability, water infiltration into the soil, or competing vegetation. Microchemical tests showed increased levels of manganese, magnesium, nitrogen, phosphorus, and calcium in the upper soil layers of burned seedbeds *(14)*.

Table 4—Potential d.b.h. of western larch trees at age 50 and at age 100 years by ecological habitat type and site index *(35)*

Ecological habitat type	Age	Site index at base age 50 years: 12.2 m or 40 ft	18.3 m or 60 ft	24.4 m or 80 ft
	yr	*cm*	*cm*	*cm*
1. *Abies lasiocarpa-Xerophyllum tenax*	50	13.7	19.3	—
	100	25.1	33.8	—
2. *Pseudotsuga menziesii*	50	14.5	19.8	—
Physocarpus malvaceus and *Calamagrostis rubescens*	100	26.7	35.	—
3. *Abies lasiocarpa-Pachistima myrsinites*	50	—[1]	20.3	25.9
	100	—	35.8	44.7
4. *Abies grandis-Pachistima myrsinites*	50	—	20.6	26.2
	100	—	36.6	45.2
5. *Tsuga heterophylla-Pachistima myrsinites* and *Thuja plicata-Pachistima myrsinites*	50	—	20.8	26.2
	100	—	36.8	45.2
	yr	*in*	*in*	*in*
1. *Abies lasiocarpa-Xerophyllum tenax*	50	5.4	7.6	—
	100	9.9	13.3	—
2. *Pseudotsuga menziesii-Physocarpus malvaceus* and *Calamagrostis rubescens*	50	5.7	7.8	—
	100	10.5	13.8	—
3. *Abies lasiocarpa-Pachistima myrsinites*	50	—	8.0	10.2
	100	—	14.1	17.6
4. *Abies grandis-Pachistima myrsinites*	50	—	8.1	10.3
	100	—	14.4	17.8
5. *Tsuga heterophylla-Pachistima myrsinites* and *Thuja plicata-Pachistima myrsinites*	50	—	8.2	10.3
	100	—	14.5	17.8

[1] Dashes indicate that values are outside the data base.

Stand density also affects height growth very early in the life of the stand *(27)*. Heavy overstocking is common in young stands with densities sometimes exceeding 86,500 trees per hectare (35,000/acre). In a 9-year-old stand at Coram Experimental Forest for example, dominant larch were growing a third faster in height in stands with 12,400 trees per hectare (5,000/acre) than they were in stands with 86,500/ha (35,000/acre). Thinning these overstocked stands relieved this height growth suppression, but even the dominant trees in unthinned stands continued to grow well below their potential in height *(30)*. By age 24, dominant trees in the thinned stands averaged more than 9 m (30 ft) tall, but their counterparts in the unthinned stands averaged 15 to 20 percent less *(29)*.

Diameter growth measured at breast height (1.37 m or 4.5 ft) for larch largely parallels height growth and is affected by many of the same factors. Larch has the potential for rapid diameter growth, but overstocking, insects, and dwarf mistletoe often prevent full realization of this potential.

Potential diameter growth curves have been developed for western larch on different combinations of habitat type and site index to provide a basis for evaluating tree and stand conditions (table 4) *(35)*.

These projections, based on relatively open trees, show larch at age 50 reaching diameters ranging from a high of 26 cm (10.3 in) on high to 14 cm (5.4 in) on low quality sites; at age 100, 45 cm (17.8 in) to 25 cm (9.9 in).

Larch diameter growth is very sensitive to stand density. For example, in 9-year-old stands on Coram Experimental Forest, overstocking of 86,500 trees per hectare (35,000/acre) had already restricted diameter growth of the dominant trees to half that of their counterparts in stands with 12,400/ha (5,000/acre) *(27)*. At age 19 and 24, dominant trees in these unthinned stands (with about 37,100/ha or 15,000/acre) continued growing at about half the rate of their counterparts in thinned stands (with about 1,000 trees per hectare or 400/acre). For example, at age 24, dominant trees in thinned stands averaged nearly 13 cm (5 in) compared to about 8 cm (3 in) for dominants in unthinned stands *(29)*. Elsewhere, 30- to 50-year-old stands in Montana showed about the same diameter relationships, with crop-trees in unthinned stands growing at about half their potential *(25)*.

Basal area increases rapidly to about age 40 years, decelerates, and nearly levels off after age 100. At age 100, basal area of larch forests approaches 69 m^2/ha (300 ft^2/acre) on high quality sites and about 46 m^2/ha (200 ft^2/acre) on low quality sites. On high sites, the average annual increase in basal area is about 0.7 m^2/ha (3 ft^2/acre) for the first century. Average increase during the 100- to 200-year period is only about one-tenth the rate noted in the first 100 years. As basal area stocking approaches site potential, increment drops off rapidly—the site is fully occupied.

Table 5—Total volume of western larch trees 1.5 cm (0.6 in) and larger in d.b.h. *(35)*

Age	Site index at base age 50 years		
	12.2 m or 40 ft	18.3 m or 60 ft	24.4 m or 80 ft
yr		*m^3/ha*	
20	[1]*17*	30	45
40	105	184	275
60	191	336	502
80	258	454	[1]*678*
100	308	544	[1]*813*
yr		*ft^2/acre*	
20	[1]*246*	434	648
40	1,494	2,632	3,934
60	2,724	4,801	7,176
80	3,680	6,484	[1]*9,692*
100	4,407	7,765	[1]*11,608*

[1] Values in italics are extrapolated beyond the range of the basic data.

Larch forests can produce heavy timber volumes. The increase in volume follows a similar pattern as basal area but peaks later. Because of their influence on diameter and height growth, site quality, age, and stocking level play the major roles in volume yield. Projected cubic yields for larch forests at age 100 range from 308 m^3/ha (4,407 ft^3/acre) on low quality to 813 m^3/ha (11,608 ft^3/acre) on high quality sites (table 5). With full stocking (but not overstocked), 544 m^3/ha (7,765 ft^3/acre) is a reasonable objective by age 100 on medium quality sites for larch forests.

Rooting Habit—Larch develops a deep and extensive root system, but little information is available about its root growth. Root lengths on first-year natural seedlings usually reach 5 cm (2 in). Under good nursery conditions, well-developed fibrous roots 20 cm (8 in) or longer develop on 1-0 growing stock. Observations in soils under young larch stands indicate extensive fibrous rooting in the top 50 cm (20 in), substantially less in the 50–100 cm (20–40 in) depths, and practically none at greater depths. Soil water depletion studies verify these observations in young larch stands *(29)*. Heavy rooting at depths greater than the above has been observed along roadcuts through old-growth stands. Evaluations of roots of windfallen overmature larch show that nearly all of them were infected with root rots *(35)*. Apparently, these rots play an important role in wind stability of overmature trees, but their importance in young trees is not known.

Reaction to Competition—Larch is the most shade-intolerant conifer in the Northern Rockies. Only during the seedling stage can it tolerate partial shading. If larch is overtopped its crown rapidly deteriorates, and its vigor declines severely.

Because of its intolerance to shade, larch grows in even-aged stands or age-classes. Its primary associates are usually the same age as larch but often give the appearance of being younger because they grow slower than larch and form the lower strata in the stand. As larch stands mature, however, shade-tolerant associates continue to establish and form younger understories.

Fire is essential to the maintenance of western larch in natural forest stands. Most fires that occur on mountain slopes are usually small and of low or moderate intensity *(8)*. Fire intensity, however, increases on steep slopes with heavy fuels, or on dry ridgetops. These fires thin stands, reduce fuels, rejuvenate undergrowth, and prepare seedbeds that promote mixed conifer stands with small pockets of regeneration dominated by seral species, particularly western larch. Intense fires often create definite even-aged stands. At Coram, multiple burns occurring at less than 50-year intervals favor lodgepole pine or shrub fields. Historically, within the mixed conifer/pinegrass communities of the Blue Mountains of Oregon, underburns occur at 10-year intervals and maintain western larch and other seral species in the stands *(15)*. Here, all species, including western larch, often overstock and can stagnate unless periodic fires release some trees. Without fire, grand fir and Douglas-fir replace the seral species.

Although larch normally remains in the dominant position, understory trees and other vegetation vigorously compete with larch for available water and nutrients. In one harvest-cutting study, diameter growth of residual mature seed trees after logging increased 67 percent over prelogging growth *(44)*. When all understory trees were also cut, the seed trees increased an additional 36 percent in diameter increment.

Even-aged silviculture systems of shelterwoods, seed-tree cuttings, and clearcuts best fit the ecological requirements of larch forests. They provide an adequate seed source and the microsite conditions needed for establishing the new seedlings. They are also compatible with the site preparations of prescribed burning or scarification needed to reduce the duff layers and vegetative competition for the new seedlings. Prescribed burning most closely approximates the natural wildfires that historically have perpetuated larch forests. No detrimental impact on site quality has been attributed to harvesting or prescribed fire on the soil microflora *(16)*.

Conversely, uneven-aged silviculture systems have limited utility in most larch forests. Not only does the residual stand show little overall growth response after partial cuttings, the growth increases that do occur are mainly on the more tolerant and generally less desirable species, such as subalpine fir. In addition, partial cuttings discriminate strongly against larch and its shade-intolerant associates in the regeneration process, and larch becomes a minor stand component in stands it formerly dominated. Prescribed burning or scarification needed to regenerate larch are very difficult in partial cuttings. For management considerations other than timber production, such as esthetics or wildlife, there may be rationale for uneven-aged silviculture systems in some larch forests. Even here, however, it should be recognized that these practices violate the normal regeneration sequence in most of these forests, accelerate the succession to tolerant species, and increase insect and disease problems. Studies on Coram Experimental Forest have demonstrated many of the problems with single-tree selection cuttings. Even with special care, it is extremely difficult to use group-selection cuttings in old-growth larch forests.

Exceptions to the above are possible in some of the drier phases of Douglas-fir and grand fir habitat types, particularly in the Blue Mountains of Oregon and some lower elevation areas of western Montana. Here, natural underburns at 20- to 30-year intervals perpetuated more open-grown stands and allowed the establishment of western larch and ponderosa pine regeneration under the main forest canopy *(1,15)*. Uneven-aged silviculture systems that mimic these natural conditions are plausible in these types of larch forests.

Thinning in young western larch stands, preferably before age 20, enhances the growth of diameter and height during the juvenile years when response potential is greatest. Drastic reduction in the densities found in most unthinned stands is advisable. Studies in young larch show that larch responds well in diameter, height, and crown retention under a fairly broad range of densities after thinning, usually exceeding what were thought to be maximum growth rates *(30)*. Even at ages 30 to 50, larch responds well to release *(25,36)*. By this age, however, overstocking has reduced the crown and response is usually delayed. Timing and extent of response is a function of length and severity of overstocking. Individual tree growth once lost can never be regained.

Branch turnups following thinning can be a problem in young larch stands. If a tree is cut off above a live branch, it may turn up, reform the tree, and reduce the effectiveness of the thinning (*35*). Older larch sometimes produce sprouts from adventitious buds on the upper bole of the tree after thinning of older stands, but this effect may not have practical significance. The amount of sprouting increases with the severity of the thinning (*25*).

Preliminary studies of fertilization in Montana (*2*) show a positive diameter growth response to fertilization with nitrogen, but the effects last only about 3 years. Similar studies in Idaho showed a short-term diameter growth response to nitrogen (*13*), but neither study showed any height increase.

Damaging Agents—Mature larches are the most fire-resistant trees in the Northern Rockies because of their thick bark, their high and open branching habit, and the low flammability of their foliage. Poles are moderately resistant, but seedlings and saplings have very little resistance to fire (*44*).

Larch is moderately to highly resistant to windthrow because of its extensive root sytem. Isolated old-growth seed trees or those along cutting boundaries, however, are susceptible to windthrow, particularly those on upper slopes and ridgetops, or those in narrow canyons and saddles where winds are channeled (*35*).

Because larch is deciduous, its branches seldom accumulate excessive amounts of either snow or ice. Early fall or late spring snows occasionally catch larch with a full complement of needles and cause severe bending. After a heavy June snow on the Coram Experimental Forest, young larch were completely flattened, but they recovered surprisingly well with little apparent long-term damage (*34*).

Young larch is extremely sensitive to noxious fumes, but because it is deciduous, the tree accumulates fewer harmful deposits than other conifers. Fluorine and sulfur dioxide are both harmful, but fluorine is the more toxic. Fluorides at levels of 30 to 35 p/m produce toxic needle effects (*5*).

Dwarf mistletoe (*Arceuthobium laricis*) is the most damaging disease-causing parasite of larch. It can infect seedlings as young as 3 to 7 years old and continue throughout the life of the tree (*49*). In addition to killing tree tops, reducing seed viability, creating conditions suitable for entry of other diseases and insects, and causing burls, brashness, and some mortality, it decreases height and diameter growth. Basal area growth reductions can be expected as follows (*22*): light infection, 14 percent; medium infection, 41 percent; and heavy infection, 69 percent.

Infected residual-stand overstories left after logging or fires promptly infect understory stands. Mistletoe seed can be ejected as far as 14 m (45 ft) (*42*). Thus 50 evenly-spaced, diseased trees per hectare (20/acre) may infest understory trees with just one crop of mistletoe seeds. Proper harvest-cutting systems, particularly clearcutting, can substantially reduce the mistletoe problem.

Three other important diseases are found in larch: needlecast caused by *Hypodermella laricis*, the quinine fungus *Fomitopsis officinalis*, and red ring rot caused by *Phellinus pini*. Many other less common but potentially dangerous fungi, such as *Encoeliopsis laricina*, infect larch but have not caused significant problems in the past (*35*).

Larch casebearer (*Coleophora laricella*) and western spruce budworm (*Choristoneura occidentalis*) are currently the two most serious insect pests of western larch (*35*). Casebearer was first detected in the Northern Rockies in 1957 and since then has spread throughout virtually the entire larch forest type (*11*). Introduced and native parasites, plus adverse weather conditions on many larch sites, appear to be reducing the casebearer problem, however. Severe defoliation by the casebearer can substantially reduce tree growth, but mortality usually is low.

Western spruce budworm has been a persistent problem wherever heavy populations of budworm overlap the range of larch (*12*). The most serious damage to larch is severance of the terminal leader, which results in an average loss of about 25 to 30 percent of the height growth for that year (*32*).

Other insect species affecting larch include the larch sawfly (*Pristiphora erichsonii*) and the larch bud moth (*Zeiraphera improbana*) that cause heavy, but sporadic, damage. The western larch sawfly (*Anoplonyx occidens*), the twolined larch sawfly (*Anoplonyx laricivorus*), and the larch looper (*Semiothisa sexmaculata incolorata*) also damage larch from time to time. Bark beetles are not generally a serious problem for larch, but the Douglas-fir beetle (*Dendroctonus pseudotsugae*) occasionally attacks weakened trees. At times, the engraver beetle (*Ips plastographus*), the larch engraver (*Scolytus laricis*), and the false hemlock looper (*Nepytia canosaria*) damage larch.

Damage from larger animals is relatively minor. Rodents, because of their seed- and seedling-eating habits, can greatly influence seedling establishment. Larch is apparently unpalatable to most big game species. In addition, most larch forests occur in areas of heavy snowpack not suitable for winter game range (*35*). Bears, however, can be a local problem. They strip the bark on the lower bole of the most vigorous trees in young sapling and pole-sized stands during the spring of the year and often kill the trees.

Special Uses

Western larch forests are valued for their multiple resource values. The seasonal change in hue of larch's delicate foliage from light green in the spring and summer, to gold in the fall, enhances the beauty of these mountain forests.

Because larch is an aggressive pioneer species, it quickly reforests areas denuded by natural or man-caused disturbances, providing protection for those important watersheds in the Columbia River Basin. Western larch is an important component of high water-yielding forests—areas where management can influence water yield through harvest cuttings *(19)* and young stand culture *(29)*.

Larch forests provide the ecological niches needed for a wide variety of birds and animals. Hole-nesting birds comprise about one-fourth of the bird species in these forests, and studies on Coram Experimental Forest show that broken-topped larch is a preferred site for the hole-nesters *(18)*. Deer, elk, moose, and the black and grizzly bear are widespread and numerous throughout the range of larch.

Larch timber is used extensively for lumber, fine veneer, long-straight utility poles, railroad ties, mine timbers, and pulpwood *(35)*. Larch wood is strong and hard and contains about 4 to 23 percent arabinogalactan. It is the best domestic source of this water soluble gum used for offset lithography and in food, pharmaceutical, paint, ink, and other industries. Arabinogalactan has the consistency of honey and contains 16 percent volatile pinene and limonene *(44)*.

Timber harvesting practices in larch forests are now utilizing more of the woody biomass formerly left in the woods after logging. Studies in the last decade have aimed at characterizing this biomass and the environmental consequences of removing biomass from larch forests *(46)*. Typically, large volumes of standing live and dead tree biomass are found in old-growth larch forests *(3)*. For example, of the 512 m^3/ha (7,318 ft^3/acre) found on a larch study area on Coram Experimental Forest in western Montana, 55 percent was in standing green trees, 20 percent in standing dead, and 25 percent in down material. In addition to tree biomass, shrubs and herbs account for additional biomass *(31)*. In terms of weight, the average total biomass was 325 t/ha (145 tons/acre) with the following distribution:

	Pct.
Standing green and dead 7.6 cm (3 in) diameter and larger	49
Crown material less than 7.6 cm (3 in) diameter	12
Down wood 7.6 cm (3 in) diameter and larger	11
Down wood less than 7.6 cm (3 in) diameter	3
Shrubs and herbs	2
Litter	1
Duff	22

Genetics

Population Differences

No differences in cold hardiness of 1-year-old larch seedlings were detected from 78 populations before frost in early September *(23)*. Regardless of geographic origin, 2-year-old seedling populations separated by 1000 m (3,300 ft) tended to differ by 1.4 days in bud burst, 1.1 weeks in bud set, and 8 cm (3.1 in) in height (21 percent of the height variance) when growing in the average test environment.

Races and Hybrids

Races of western larch are not known. Putative natural hybridization of western larch and subalpine larch *(Larix lyallii)* occasionally occurs in areas where their distributions overlap *(4)*. Even where the geographic ranges of the two species overlap, usually elevations of 300 m (1,000 ft) or more separate them. Interspecific hybrids of western larch and Japanese larch *(Larix leptolepis)* were taller and more vigorous than open-pollinated western larch progenies at the end of the first and second growing seasons *(48)*.

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Libocedrus decurrens Torr. Incense-Cedar

Cupressaceae Cypress family

Robert F. Powers and William W. Oliver

Incense-cedar *(Libocedrus decurrens)* is the only species from the small genus *Libocedrus* that is native to the United States. Increasingly, it is placed in a segregate genus *Calocedrus*. Incense-cedar grows with several conifer species on a variety of soils, generally on western slopes where summer conditions are dry. It is long-lived and grows slowly. Most of the top-grade lumber is used for the manufacture of pencils and exterior siding.

Habitat

Native Range

Incense-cedar (fig. 1) is a distinctive component of the Sierra Nevada mixed-conifer forest, where it grows as scattered individuals or in small groups *(5)*. Its range spans about 15° of latitude and a variety of climates from the southern slope of Mount Hood in Oregon, southward through the Siskiyou, Klamath, and Warner Mountains, Cascade and Coast Ranges, and Sierra Nevada to the dry Hanson Laguna and Sierra de San Pedro Martir Ranges in Baja California *(7)*. Incense-cedar grows from the coastal fog belt eastward to the desert fringes. It can be found in the Washoe Mountains of west–central Nevada *(12)*.

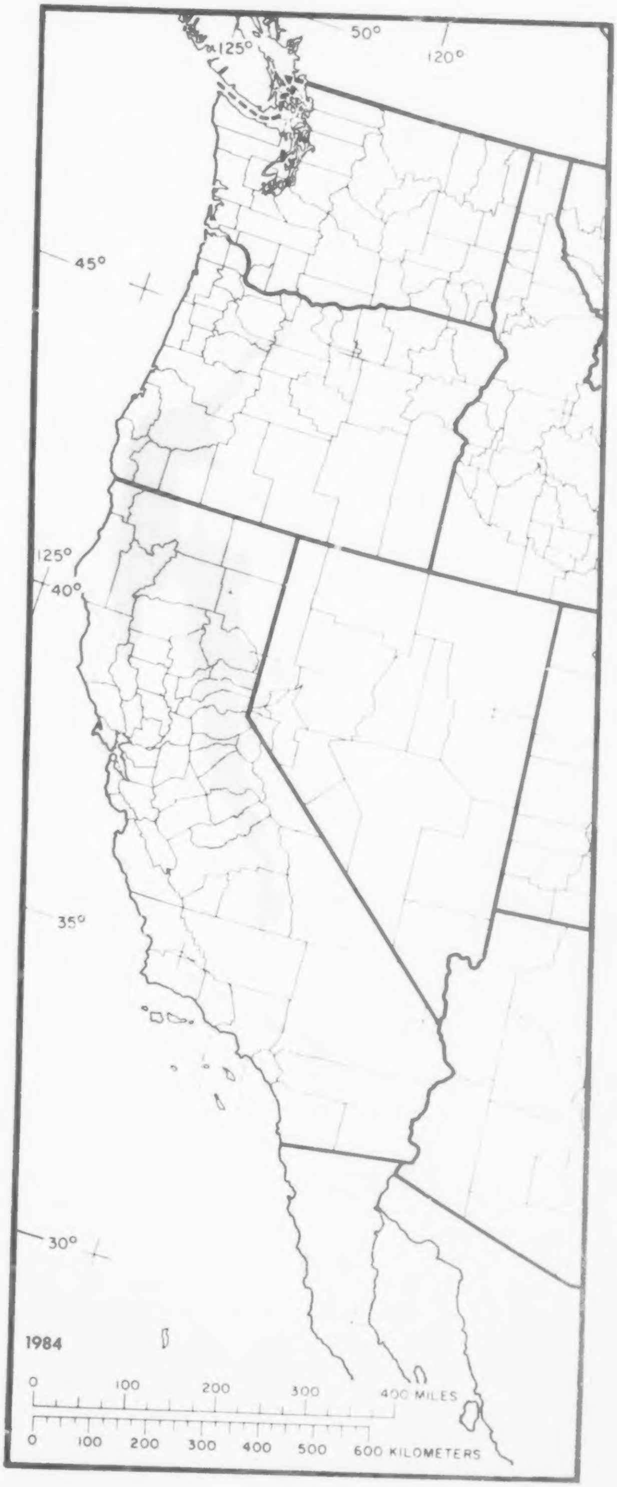

Figure 1—*The native range of incense-cedar.*

Climate

Incense-cedar's natural range is characterized by dry summers, usually with less than 25 mm (1 in) precipitation per month; annual temperature extremes are −34° to 48° C (−30° to 118° F). Annual precipitation, part of which is snow, varies from 510 to 2030 mm (20 to 80 in). Precipitation may be as low as 380 mm (15 in) a year for incense-cedar found on the east side of the Cascades and in the Warner Mountains in Oregon and California *(22)*.

Soils and Topography

Incense-cedar grows on many kinds of soils developed from a wide variety of parent rocks—rhyolite, pumice, andesite, diorite, sandstone, shale, basalt, peridotite, serpentinite, limestone, and

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granitic or metamorphic equivalents. It is particularly adept at extracting soil phosphorus *(21)* and calcium *(35)*, and excluding surplus magnesium.

Soils supporting incense-cedar vary greatly. Reaction ranges from nearly neutral to strongly acid. Textures vary from coarse sands to very fine clays. The best stands generally are found on deep, well-drained, sandy loam soils developed on granitic rocks and sandstone; deep clay loams developed on basalt and rhyolite; and occasionally on deep, coarse-textured, well-drained soils developed from pumice.

In California, incense-cedar grows best on deep, slightly to moderately acid Ultic Haploxeralfs, such as the Holland series weathered from granitic rock (fig. 2), and the Cohasset series derived from andesite and basalt. Incense-cedar also grows on infertile soils derived from peridotite or serpentinite throughout the Sierra Nevada and tends to be restricted to these soils in western portions of the north Coast Ranges and Klamath Mountains *(7)*. Although it is a good competitor on these soils because of its apparent ability to extract calcium and exclude magnesium, its growth is considerably less than on more fertile sites. Apparently the high calcium-extracting ability of incense-cedar may interfere with magnesium and micronutrient uptake on limestone. Incense-cedars are rare on limestone soils, and the trees that do grow there contain high concentrations of calcium and low concentrations of manganese and zinc *(35)*.

Incense-cedar grows at elevations between 50 and 2010 m (165 and 6,600 ft) in its northern extreme *(30)*, and between 910 and 2960 m (3,000 to 9,700 ft) in its southern limits. In the Sierra Nevada, the tree grows best at elevations between 610 and 2100 m (2,000 to 6,900 ft). Once established, incense-cedar is a good competitor on hot, dry sites and commonly shares an upper canopy position on southwestern slopes. On cooler, moister aspects, it is usually subdominant to other species.

Associated Forest Cover

Rarely found in pure stands, incense-cedar grows in several forest cover types where it occupies a subdominant crown position. Except in Sierra Nevada Mixed Conifer (Society of American Foresters Type 243) *(5)* where its stocking may account for half of the stems in a stand *(20,26)*, incense-cedar is a minor component of the cover types in which it is found. These cover types include Pacific Douglas-Fir (Type 229), Pacific Ponderosa Pine–Douglas-Fir (Type 244), California Black Oak (Type 246), Jeffrey Pine (Type 247), and Pacific Ponderosa Pine (Type 245). Southern and drier portions of the types Oregon White Oak (Type 233) and Douglas-Fir–Tanoak–Pacific Madrone (Type 234) as well as inland extensions of Port-Orford-Cedar (Type 231) also contain incense-cedar.

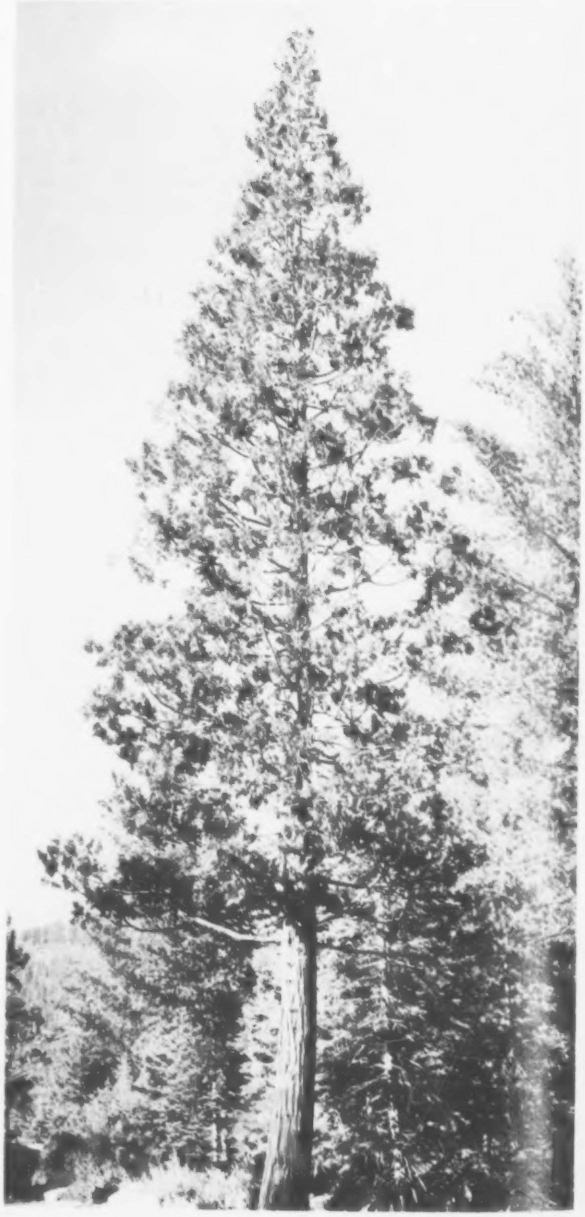

Figure 2—*Young-growth incense-cedar growing in soil derived from granitic rock in the central Sierra Nevada of California.*

In the northern part of its range, incense-cedar often is found with coast Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)*, ponderosa pine *(Pinus ponderosa* var. *ponderosa)*, sugar pine *(P. lambertiana)*, western white pine *(P. monticola)*, Jeffrey pine *(P. jeffreyi)*, California white fir *(Abies concolor* var. *lowiana)*, grand fir *(A. grandis)*, western hemlock *(Tsuga heterophylla)*, western redcedar *(Thuja plicata)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, Oregon white oak *(Quercus garryana)*, California black oak *(Q. kelloggii)*, tanoak *(Lithocarpus densiflorus)*, giant chinkapin *(Castanopsis chrysophylla)*, and Pacific madrone *(Arbutus menziesii)*. In the central part, it grows with coast Douglas-fir, ponderosa pine, sugar pine, Jeffrey pine, Sierra lodgepole pine *(Pinus contorta* var. *murrayana)*, California white fir, California red fir *(Abies magnifica)*, giant sequoia *(Sequoiadendron giganteum)*, California black oak, tanoak, giant chinkapin, and Pacific madrone. In the southern part, common associates are Jeffrey pine, ponderosa pine, sugar pine, Coulter pine *(Pinus coulteri)*, bigcone Douglas-fir *(Pseudotsuga macrocarpa)*, and California black oak. Tree associates on ultramafic soils include Jeffrey pine, western white pine, sugar pine, knobcone pine *(Pinus attenuata)*, and coast Douglas-fir.

Common brush species growing with incense-cedar are greenleaf manzanita *(Arctostaphylos patula)*, mountain whitethorn *(Ceanothus cordulatus)*, deerbrush *(C. integerrimus)*, snowbrush *(C. velutinus)*, littleleaf ceanothus *(C. parvifolius)*, bearclover *(Chamaebatia foliolosa)*, bush chinkapin *(Castanopsis sempervirens)*, salal *(Gaultheria shallon)*, and coast rhododendron *(Rhododendron californicum)* *(22)*. On ultramafic soils, sclerophyllous shrubs predominate and include barberry *(Berberis pumila)*, silk-tassel *(Garrya buxifolia)*, tanoak, huckleberry oak *(Quercus vaccinifolia)*, coffeeberry *(Rhamnus californica)*, western azalea *(Rhododendron occidentale)*, and red huckleberry *(Vaccinium parvifolium)* *(32)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Yellow-green, pollen-bearing strobili are borne terminally on twigs as early as September and reach a length of about 6 mm (0.25 in) at pollen shed in late winter to early spring. Incense-cedar is monoecious; both male and female flowers may be borne on the same twig. Cones, inconspicuous in spring, are pendent and 20 to 40 mm (0.8 to 1.5 in) long when they mature in late summer. They are composed of three pairs of opposing leathery scales. Two of the six scales become greatly enlarged and form a cover around the two scales that bear the seeds. Each seed has two wings of unequal length. Embryos have two cotyledons.

Seed Production and Dissemination—Although incense-cedars are considered prolific seed producers, medium to heavy seed crops are borne at intervals usually averaging 3 to 6 years. Sometimes, cone crops are absent entirely *(22)*. In a southwestern Oregon study, medium to abundant crops appeared in only 3 years, and light or no crops were found in 12 of the 15-year reporting period *(28)*. As many as 961,500 seeds per hectare (389,100/acre) may fall during heavy production years *(22)*. Geographic variability in cone and seed production is great *(23)*. Seed dispersal begins in late August at the lowest elevations and in October at higher levels. Although seedfall may extend into winter months, seed soundness seems unrelated to time of dispersal (table 1).

Incense-cedar seeds average 33,100/kg (15,000/lb) and vary from 14,100 to 63,900/kg (6,400 to 29,000/lb). Averages for collections from the northern and central part of incense-cedar's range vary from 29,800 to 44,500/kg (13,500 to 20,200/lb) *(28)*. Because they are light in weight and have a large wing (averaging 2.5 cm (1 in) in length and nearly one-third that in width), seeds of incense-cedar fall slowly (1.8 m/s, or 5.9 ft/s, in still air) *(22)*, and are carried great distances by wind.

Seedling Development—Germination may be doubled by stratifying seeds at 3° to 5° C (37° to 41° F) for 30- to 60-day periods, although results are not always consistent. Germination under controlled conditions may be as much as 98 percent but usually averages 20 to 40 percent *(28)*. These values are similar to those found under field conditions *(22)*. Germination is epigeal *(28)*. In nature, incense-cedar

Table 1—Incense-cedar seedfall as measured from traps on the Stanislaus National Forest, CA *(22)*.

Measurement date	Percent of all seed trapped	Percent sound seed
1937		
October 6	11	3
October 27	36	37
November 11	53	60
1940		
October 11	32	54
October 29	34	38
November 13	34	8

germinates on a wide range of surface conditions. Although survival is best under partial shade *(22)*, incense-cedar seedlings survive over a broader array of site conditions than do most conifers *(22,26)*.

Initial rates of root growth are slow to moderate in incense-cedar compared with other species. In the first season, primary roots may extend to a depth of 30 cm (12 in), compared with as much as twice that length for ponderosa pine and sugar pine *(22)*. Incense-cedar, therefore, is particularly susceptible to drought on exposed sites during the first year. Root systems develop rapidly, however, and by the end of the second year, lateral and tap root lengths compare well with ponderosa pine *(29)*. In an artificially controlled study *(33)*, seedling roots showed a peak of growth in the spring, with rates averaging 3 to 5 mm (0.12 to 0.20 in) per day. Growth slowed in midsummer, but increased again in fall, averaging 1 to 3 mm (0.04 to 0.12 in) per day between October and December. Activity cycles varied for individual roots. Not all roots were active at any one time.

Incense-cedar lacks the distinct spring flush typical of many temperate conifers. Successive years' growth is not easily seen along the stem. Instead, elongation of several leaf internodes near the shoot tip in fall is arrested over winter and is not completed until the following spring. Hence, shoot growth is a more or less continuous process characterized by changes in tempo that are influenced primarily by current environment *(9)*.

On the Stanislaus National Forest in the central Sierra Nevada, CA, at an elevation of 1600 m (5,250 ft), seasonal height growth of incense-cedar started an average of 11 days later than ponderosa pine, was similar to sugar pine, but averaged 31 days earlier than white fir *(22)*. At Challenge Experimental Forest, 1° 30′ of latitude farther north in the Sierra Nevada and 810 m (2,660 ft) lower in elevation, sugar pine and ponderosa pine began height growth 3 to 5 weeks sooner than incense-cedar, and white fir began a week later *(21)*. On the Stanislaus National Forest, the height growth period for incense-cedar lasts an average of 91 days, a period greater than for any other native species. At Challenge Experimental Forest it lasted 112 days but stopped sooner than the height growth period for ponderosa or sugar pine.

Seasonal radial growth starts before height growth. On the Stanislaus National Forest, growth begins about April 15, some 2 weeks later than at Challenge. At both locations, however, incense-cedar begins radial growth at about the same time as ponderosa and sugar pine, but 2 weeks earlier than white fir. At both locations, the period of diameter growth for incense-cedar is second only to that for ponderosa pine, lasting 136 days at Stanislaus and 146 days at Challenge *(21,22)*.

Table 2—Height growth of conifer seedlings relative to ponderosa pine under several silvicultural systems

Silvicultural system	Ponderosa pine	Incense-cedar	Sugar pine	White fir	Douglas fir
Selection[1]					
Single-tree	1.00	1.80	2.00	2.80	1.40
Group	1.00	0.90	1.50	1.50	1.50
Shelterwood[1]	1.00	0.70	0.96	1.07	0.78
U.A.C.[2]	1.00	0.22	0.70	0.25	—
Clearcut					
Natural[1]	1.00	0.00	0.89	0.65	0.68
Planted[3]	1.00	0.71	0.56	0.41	0.55

[1] Nine-year-old naturally regenerated seedlings, Challenge Experimental Forest, CA. Group selection openings were 9 to 27 m (30 to 90 ft) in diameter (13).

[2] Average of all natural seedlings regenerating in 12 years after Unit Area Control cuttings, Stanislaus National Forest, CA (26).

[3] Six-year-old seedlings from local seed, Challenge Experimental Forest, CA (21).

Naturally regenerated incense-cedar grows slowly because of low sunlight or heavy browsing, often taking 3 to 5 years to reach a height of 8 to 15 cm (3 to 6 in). Although increased sunlight favors height growth, poor initial root development of naturally regenerated incense-cedar and preferential browsing by deer may mask its ability to respond to increased light, compared with other species (table 2).

Incense-cedar raised from local seed and planted as 1-0 stock in a fresh clearcut at Challenge Experimental Forest, however, grew faster than three other species, and at 6 years from planting was second only to ponderosa pine in both height and standing biomass *(21)*. Apparently, the well-developed root systems of planted seedlings provide enough water uptake to sustain vigor, which helps seedlings resist browsing pressure.

Established incense-cedar seedlings are remarkably drought tolerant. The species has been ranked more tolerant than sugar pine or ponderosa pine, Douglas-fir, or grand fir when grown in pumice, and second only to ponderosa pine when grown in sand *(19)*. The tolerance was attributed to a complete occupancy of the soil mass by incense-cedar roots. In a controlled experiment, artificial dew more than doubled the survival period of incense-cedar seedlings grown in soils dried to permanent wilting point *(31)*. Dew helped incense-cedar tolerate drought better than ponderosa pine and Jeffrey pine, although pines were more tolerant when dew was withheld. At Challenge Experimental Forest, predawn measurements of xylem moisture tension in September showed that incense-cedar, ponderosa pine, and sugar pine were similar to each other and significantly lower in water stress than Douglas-fir or white-fir *(21)*.

Although drought may kill many first-year seedlings, particularly on compacted landings and skid trails, insects usually account for greater losses. Cutworms destroy many seedlings. Rodents are generally of only minor importance. During a 5-year period, 53 percent of the 1- to 2-month-old incense-cedar seedlings on Stanislaus National Forest plots were destroyed by cutworms *(Noctuidae* larvae) *(22)*. The seed-to-seedling ratio on four cutover plots varied from 20:1 to 355:1 *(22)*. Seedling tap roots may be damaged by root rot, but recovery can be rapid and tops may show no sign of attack *(27)*.

Vegetative Reproduction—Incense-cedar does not reproduce vegetatively in nature, but can be stimulated to do so in the greenhouse *(18)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Incense-cedar varies greatly in size in different parts of its range. In the Coast Ranges and in southern California, the largest trees generally are from 18 to 24 m (60 to 80 ft) tall and 90 to 120 cm (36 to 48 in) in d.b.h. In the Sierra Nevada, incense-cedars frequently grow to heights near 46 m (150 ft) with d.b.h.'s near 210 cm (84 in). The largest tree measured was 375 cm (148 in) in d.b.h. *(1)*. A tree 69 m (225 ft) tall was reported from southern Oregon. At high elevations, especially on dry, exposed sites, trees tend to be small and scrubby.

Incense-cedar is long-lived. Large trees often are more than 500 years old *(22)*. The oldest recorded age is 542 years for a tree only 130 cm (51 in) in d.b.h.

Growth rates of young mixed conifer stands in the central Sierra Nevada were investigated recently *(3)*. In stands with basal areas of 23 to 69 m^2/ha (100 to 300 $ft^2/acre$), periodic annual increment of incense-cedar was 0.81 cm (0.32 in) in d.b.h. and 0.3 m (1.0 ft) in height at age 40. By age 90, periodic annual increment had declined to 0.36 cm (0.14 in) for d.b.h. and 0.2 m (0.6 ft) for height.

Incense-cedar often grows more slowly than associated conifers and is therefore a major component of the intermediate and suppressed crown classes. Seldom does it contribute more than 5 to 10 percent of the stand volume *(22)*. At Blodgett Forest in the northern Sierra Nevada, for example, volume growth of incense-cedar was consistently slower than its associates, regardless of stand density or tree size *(4)*. In stands of moderate density, incense-cedar grew in volume at an annual rate of 1.6 percent, compounded. The average rate for all species was 2.3 percent. On poor sites, however, open-grown incense-cedars as large as 60 cm (24 in) in d.b.h. can exceed all other species, except white fir, in basal area growth *(22)*. On better sites, incense-cedars generally fall behind and are forced to endure more and more shade. Increasing shade further slows their growth to the point of bare existence. On such trees, 16 annual rings per centimeter (40/in) of diameter are not uncommon *(12)*.

Rooting Habit—From seedling stage through maturity, incense-cedar has a more spreading and extensive rooting habit than many of its associates. This extensive, well-developed root system allows it to survive droughty sites and resist windthrow. Root branching of seedlings in an artificially controlled environment was inversely proportional to growth rate *(33)*. Rapidly growing roots produced few laterals, but when growth of these roots temporarily ceased, laterals were produced in profusion. When growth resumed, laterals again were widely spaced, resulting in a node-internode pattern.

Reaction to Competition—Incense-cedar has been rated as more shade tolerant *(22)* than the associated pines and Douglas-fir *(16)*, and perhaps less tolerant than white fir and grand fir. In the seedling stage, incense-cedar can endure dense shade, especially in cool, moist environments *(17)*. But for full development from sapling stage through maturity, it requires more light *(22)*.

Incense-cedar shows good response to release. Much of the extremely slow growth of young reproduction results from suppression or browsing. When released, seedlings grow rapidly in height. But because height growth usually is slower than that of associated species of comparable age, incense-cedar usually is a secondary species in the final stand *(22)*. Although shaded out, lower branches are slow to shed, even in dense stands. Many dead branches must be removed, therefore, if clear lumber is to be produced in rotations of 80 to 120 years.

Damaging Agents—Overmature incense-cedars are more defective than their associates. The amount of cull increases with age of the trees and varies among stands *(22)*. Average cull percents based upon gross volume are 4 to 6 percent for immature dominants, 21 percent for mature dominants, and 68 to 77 percent for overmature dominants.

The single most destructive agent affecting incense-cedar is the pocket dry rot *(Tyromyces amarus)*. Pocket dry rot is most common in trees growing on good sites. In parts of the Sierra Nevada, 75 to 100 percent of the mature trees are infected. Trees on marginal sites near incense-cedar's eastern limit usually are infected less *(2)*.

The spores of pocket dry rot must be deposited on an open wound to infect trees because the mycelium cannot penetrate through the bark into the heartwood *(14)*. The most prevalent port of entry is through fire scars (84 percent). Knots (10 percent) are next in frequency and injuries resulting from lightning and frost (6 percent) are least *(22)*. Pocket dry rot seems relatively resistant to heartwood extractives that are toxic to other heart-rotting fungi and may actually detoxify them *(34)*. This unusual ability may explain the apparent anomaly of highly defective heartwood in live, overmature trees and high durability of heartwood in sawn products.

In management of young-growth incense-cedar, the age at which dry rot begins to cause losses is of primary significance. Suppressed trees are subject to severe dry rot infection after they reach 165 years, but dominant trees generally are safe until 210 years old *(22)*. Because the rotation age of young-growth stands is considerably less than these critical ages, pocket dry rot should not cause severe cull in managed stands. Two other fungi that occasionally rot the heartwood of living incense-cedar are *Phellinus pini* and *Phaeolus schweinitzii (10)*.

Root disease kills more incense-cedar trees than any other pathogen *(24)*. Of the three facultative, parasitic fungi found attacking incense-cedar roots, *Armillaria* sp., *Heterobasidion annosum*, and *Phellinus weiri*, probably the most destructive is *Heterobasidion annosum*. More than 100 *H. annosum* infection centers have been confirmed on developed sites in Yosemite Valley, CA *(25)*. Property damage caused by falling root-diseased trees has been substantial and has led to the development of a risk-rating system. On the basis of crown characteristics, the system predicts the potential for early failure of root-diseased incense-cedar *(25)*.

The only foliage disease of any consequence is the rust caused by *Gymnosporangium libocedri (10)*, which infects incense-cedar of all ages, causing witches' brooms, but only infrequently kills smaller branches. Although extensive infections of leaf rust retard growth, no deaths have been attributed directly to the disease. Infections in the main stem may result in burls that cause defect in lumber *(2)*.

Ozone, the major plant-damaging constituent of photochemical oxidant air pollution, injures the foliage of many coniferous species. Incense-cedar is insensitive to injury from ozone. It appears to have sufficient numbers of tolerant individuals so that it may be planted with reasonable success in the ozone-affected forests common in the southern portion of this species' natural range *(15)*.

Incense-cedar mistletoe *(Phoradendron juniperinum* subsp. *libocedri)* grows on incense-cedar throughout the range of the tree. This true mistletoe causes elongated swellings on the branches and occasionally on the trunk. Severe infections suppress growth but rarely kill large trees *(2)*.

Many species of insects are found on incense-cedar, but relatively few cause serious losses. A cone sawfly *(Augomonoctenus libocedrii)* sometimes infests cones, resulting in damage resembling that of cone-feeding caterpillars *(6)*. The juniper scale *(Carulaspis juniperi)* is a European species now distributed throughout the range of incense-cedar *(6)*. It attacks twigs, leaves, branches, and cones, causing the foliage to turn yellow. Sometimes branches and entire trees are killed. Six species of cedar bark beetles *(Phloeosinus* spp.) can be found working under bark of trunks, tops, and limbs of weakened, dying, or felled trees or of broken branches *(6)*. Although damage usually is inconsequential, beetles occasionally become sufficiently numerous and aggressive to attack and kill apparently healthy trees. Several wood borers have been found in incense-cedar, but none poses a threat to the life of the tree *(6)*. The flatheaded cedar borer *(Chrysobothris nixa)* mines the bark and outer wood of limbs, trunks, and roots of weakened, dying, and dead trees, principally in the coast region. The amethyst cedar borer *(Semanotus amethystinus)* is similar to *Chrysobothris nixa* but confines its work to the inner bark and a scoring of the outer sapwood of boles and large limbs throughout the range of incense-cedar. The western cedar borer *(Trachykele blondeli)*, like *Chrysobothris nixa*, can cause serious degrade and cull in trees cut for products requiring sound wood. Its larvae mine the sapwood and heartwood of living trees. *Trachykele opulenta* is similar to *T. blondeli* but less destructive. The incense-cedar wasp *(Syntexis libocedrii)* bores in the sapwood of fire-scorched trees in California.

Fire has played a significant role in the health and relative abundance of incense-cedar in mixed-conifer stands. Sapling incense-cedars are more readily killed by fire than most of their associates; the thick bark of mature incense-cedar offers considerable protection from fire. Intense fires indirectly result in more damage to mature trees, however, by exposing trunks to infection by pocket dry rot. As a result of fire control by land management agencies beginning about 1900, and partial cutting practices, the proportion of incense-cedar in the understory has increased. Incense-cedar is favored because it is a prolific seeder and because the shade-tolerant seedlings and saplings can persist for long periods in the understory.

Special Uses

The outstanding durability and resistance to decay of lumber from incense-cedar heartwood make it ideal for exterior use where moisture is present. This wood gives long service with little maintenance in such uses as mud sills, window sashes, sheathing under stucco or brick veneer construction, greenhouse benches, fencing, poles, and trellises *(12)*. Incense-cedar also is used extensively for exterior siding because it is dimensionally stable and holds paint well, in addition to being durable.

Rich color, sound knots, and aromatic fragrance make the wood popular for interior paneling and woodwork. At present, pecky cedar (boards sawn from trees infected with pocket dry rot) is in demand for paneling and backyard fencing, thereby making a market for poor quality grades that formerly were not utilized.

Incense-cedar is ideally suited to the manufacture of pencils because it is soft, easily whittled, and has straight grain *(12)*. Much of the top-grade lumber produced goes to this use.

Incense-cedar is cultivated widely as an ornamental tree both within its natural range and as an introduced species. The tree grows well in western and central Europe *(11)* and in the Eastern United States as far north as Massachusetts.

Genetics

A few horticultural varieties are recognized. In southern California, especially in southwestern San Bernardino County, trees with conspicuously narrower crowns and more spire-like silhouettes than those of the Sierra Nevada are common. European experience with incense-cedar as an ornamental suggests that the columnar trees from southern California may be more sensitive to cold than are the trees from northerly sources *(11)*.

The genetic structure of incense-cedar was studied in stands that occupy different elevations and aspects within each of three locations in the southern Cascades and Sierra Nevada *(8)*. Genetic variation was assessed using two approaches: measuring characteristics of seedling growth and estimating allele and genotypic frequencies. Conclusions were similar for both approaches. Genetic diversity was as great among local stands as among regions, and no consistent pattern could be related to elevational or aspect differences. Growth in height and branch length was less for southern sources. Striking differences among provenances, however, like those found for Douglas-fir, lodgepole pine, and white fir, were not apparent.

No hybrids of incense-cedar are known.

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Picea breweriana Wats. **Brewer Spruce**

Pinaceae **Pine family**

Dale Thornburgh

Brewer spruce *(Picea breweriana)*, named for its first collector, is often considered "mysterious" because this attractive conifer is found on seldom-visited high mountain ridges and steep north slopes. Its other common name, weeping spruce, is derived from the distinctive feature of many ropelike branchlets that hang in a fringe from all but the topmost slender horizontal limbs. This branching habit results in many knots in the wood, which has little commercial importance.

Habitat

Native Range

Brewer spruce (fig. 1) is found only in the mountains of northwestern California and southwestern Oregon near the Pacific coast between latitudes 40° 50′ N. and 42° 40′ N. The best developed stands are on the high ridges of the western Siskiyou Mountains in California and Oregon. Other concentrations are found on high ridges and in upper valleys of the Marble, Salmon, and Trinity Mountains of California *(7)*. Throughout the rest of the range, Brewer spruce grows as a single tree and as scattered small populations in valleys and on ridgetops *(9,12,16)*.

Climate

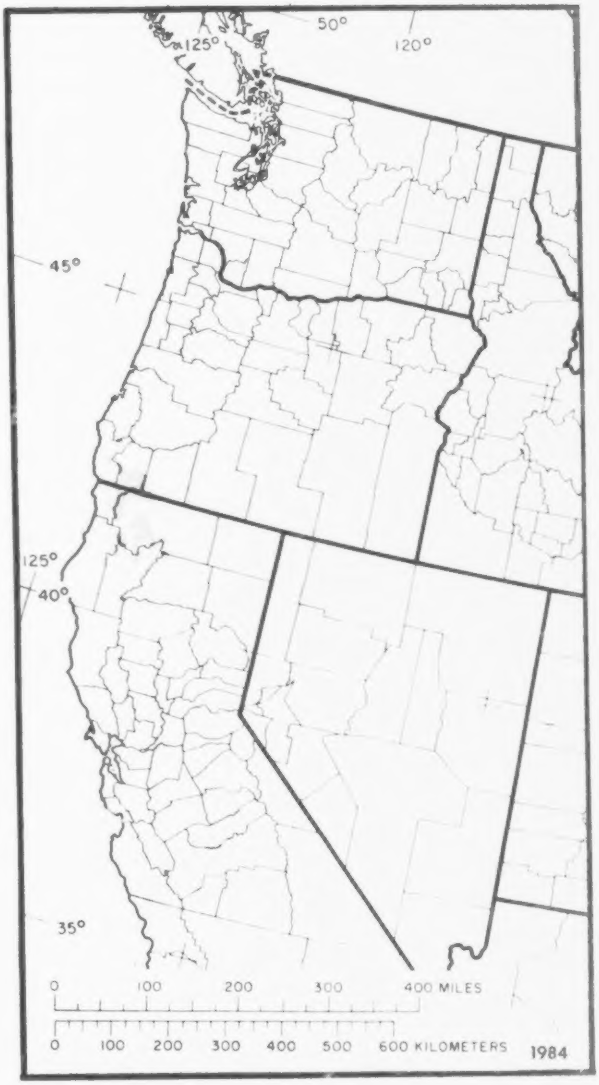

Figure 1—*The native range of Brewer spruce.*

The range of Brewer spruce is primarily influenced by the maritime climate of the Pacific Ocean: cool, wet winters and warm, relatively dry summers. The climate changes drastically, however, from west to east across the range of Brewer spruce, which is 113 km (70 mi). On the most westerly ridge occupied by Brewer spruce, average annual precipitation is more than 2800 mm (110 in); farther east, it is less than 1000 mm (39 in). Most of the precipitation falls as winter rain or snow; less than 5 percent occurs in the summer. The amount of snowfall and accumulated snowpack varies greatly from year to year and geographically across the range. A few stands of Brewer spruce in valleys receive no snow some years, whereas other stands accumulate up to 4 to 5 m (13 to 16 ft) *(5)*. Humidity is high in the western part of the range and relatively low in the eastern part. Summer fog is common along the westernmost ridges and valleys. Summer thunderstorms are common in the eastern portion of the range. Temperatures also vary widely. In the western portion, the mean temperature in January is 5° C (41° F); in July, 11° C (52° F). On the eastern edge of the range, the mean temperature is −1° C (30° F) in January and 20° C (68° F) in July.

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The varied climate indicates that Brewer spruce has an ecological amplitude that should enable it to obtain a wider and more contiguous distribution. Its sensitivity to fire seems to have restricted its range *(13)*.

Soils and Topography

Brewer spruce grows on a wide variety of geologic parent materials and soils. It is found on soils developed from sedimentary, granitic, serpentine, and metavolcanic rocks. Most of the large stands of Brewer spruce are found on shallow, rocky, undeveloped soils of the order Entisols; a few stands are on deeper, well-developed soils. Throughout its range, Brewer spruce is never found in areas where the soils are saturated during the growing season. It appears to be generally restricted from the more fertile soils by competition from true firs *(Abies* spp.). Brewer spruce is more abundant on less fertile soils.

Brewer spruce is found on most topographic locations—ridgetops, north- and south-facing slopes, benches, and valley bottoms. The only habitat restriction is boggy or wet areas. The apparently preferred location is the steep, north-facing slopes where the largest stands are located. In the western Siskiyou Mountains, these locations are north slopes near the tops of the ridges, but in the eastern Salmon Mountains, the largest stands are on middle, north-facing slopes. Brewer spruce is found from elevations of 700 to 2100 m (2,300 to 6,900 ft) in the western Siskiyou Mountains and from 1370 to 2290 m (4,500 to 7,500 ft) in the eastern Klamath region.

Associated Forest Cover

Brewer spruce grows with a wide variety of associated plants and vegetation types in the montane and subalpine forests of the Klamath region. Although it grows throughout the region, its range is one of local, disjunct populations of various sizes. In some areas, it is an occasional climax tree species in mixed stands dominated by California red fir *(Abies magnifica)*, white fir *(A. concolor)*, or mountain hemlock *(Tsuga mertensiana)*. In other areas, it grows in small, pure, dense stands on north-, east-, and west-facing slopes. It is also found as individuals invading seral pine stands and montane chaparral. In the Siskiyou Mountains, Brewer spruce seedlings and saplings are found in montane chaparral on all aspects. It is associated with Sadler oak *(Quercus sadleriana)*, huckleberry oak *(Q. vaccinifolia)*, and greenleaf manzanita *(Arctostaphylos patula)*.

Some of the best-developed stands of Brewer spruce are located on moderate east- and west-facing slopes with deep soil. These forests in the California red fir/Sadler oak habitat have a 70 to 80 percent canopy cover. Density of trees over 10 cm (4 in) in d.b.h. is 125 to 320 Brewer spruce per hectare (50 to 130/acre), 30 to 95 white fir per hectare (12 to 39/acre), 10 to 70 Douglas-fir *(Pseudotsuga menziesii)* per hectare (4 to 28/acre), 0 to 10 sugar pine *(Pinus lambertiana)* per hectare (0 to 4/acre), and 5 to 60 California red fir per hectare (2 to 24/acre). The total basal area ranges from 35 to 54 m²/ha (153 to 235 ft²/acre). Dense reproduction is present in the tolerant conifers: Brewer spruce, California red fir, and white fir; Brewer spruce has about one-third the total number of seedlings under 180 cm (70 in) in height.

Brewer spruce is an element of the following vegetation habitat types of the Klamath region *(2,12,13,14)*. Plants of major importance are listed for each type.

- *Abies concolor* zone, Siskiyou Mountains

Abies concolor/Vaccinium membranaceum (white fir/thinleaf huckleberry) habitat type. Brewer spruce is a minor climax species. Other shrubs: Sadler oak.

Abies concolor/Pachistima myrsinites (white fir/Oregon boxwood) habitat type. Brewer spruce is often a codominant climax species. Other trees: Douglas-fir and sugar pine. Other shrubs: Sadler oak, Oregongrape *(Berberis nervosa)*. Other herbs: western prince's-pine *(Chimaphila umbellata)*, rattlesnake plantain *(Goodyera oblongifolia)*, and vanillaleaf *(Achlys triphylla)*.

Chamaecyparis lawsoniana/Rhododendron occidentale (Port-Orford-cedar/western azalea) habitat type. Brewer spruce is often a minor climax species. Other trees: western white pine *(Pinus monticola)*. Other shrubs: Sadler oak.

- *Abies concolor* zone, central Klamath region

Abies concolor/Chimaphila umbellata (white fir/western prince's-pine) habitat type. Brewer spruce occasionally occurs as a minor climax species. Other trees: Douglas-fir, sugar pine, ponderosa pine *(Pinus ponderosa)*, and incense-cedar *(Libocedrus decurrens)*. Other shrubs: western hazel *(Corylus cornuta)*, wood rose *(Rosa gymnocarpa)*, and snowberry *(Symphoricarpos hesperius)*.

- *Abies magnifica* zone, Siskiyou Mountains

Abies magnifica/Quercus sadleriana (California red fir/Sadler oak) habitat type. Brewer spruce often occurs as a minor climax species. Other trees: white fir, Douglas-fir, western white pine, and sugar pine. Other shrubs: thinleaf huckleberry.

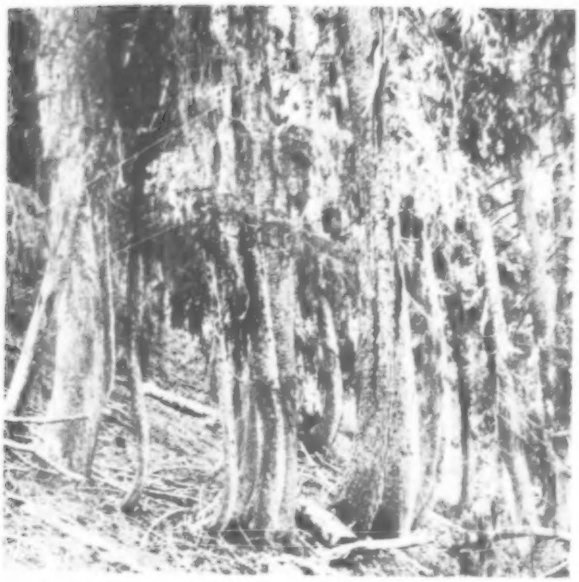

Figure 2—*Dense stand of Brewer spruce in the* Abies magnifica *zone of the Siskiyou Mountains.*

Abies magnifica/Arctostaphylos nevadensis (California red fir/pine mat manzanita) habitat type. Brewer spruce occasionally occurs as a codominant climax species. Other trees: western white pine. Other shrubs: Sadler oak and greenleaf manzanita.

Picea breweriana/Quercus vaccinifolia (Brewer spruce/huckleberry oak) habitat type. Brewer spruce occurs as a codominant climax species. Other trees: western white pine, California red fir, Douglas-fir, and incense-cedar. Other shrubs: greenleaf manzanita, pine mat manzanita, and Sadler oak.

Picea breweriana/Quercus sadleriana (Brewer spruce/Sadler oak) habitat type. Brewer spruce occurs as the dominant climax species (fig. 2). Other trees: western white pine and white fir. Other shrubs: huckleberry oak and thinleaf huckleberry.

- *Abies magnifica* zone, central and eastern Klamath region

Abies magnifica/Leucothoe davisiae (California red fir/mountain laurel) habitat type. Brewer spruce is an occasional minor climax species. Other trees: white fir, lodgepole pine *(Pinus contorta)*, western white pine, and mountain hemlock *(Tsuga mertensiana)*. Other shrubs: swamp current *(Ribes lacustre)*, mountain alder *(Alnus tenuifolia)*, and mountain ash *(Sorbus californica)*. Other herbs: groundsel *(Senecio triangularis)*, queenscup *(Clintonia uniflora)*, starflower *(Trientalis latifolia)*, trillium *(Trillium ovatum)*, and false Solomon's seal *(Smilacina stellata)*.

Abies magnifica/Linnaea borealis (California red fir/twinflower) habitat type. Brewer spruce is an occasional codominant climax species in open forest stands. Other trees: Douglas-fir, white fir, western white pine, mountain hemlock, sugar pine, ponderosa pine, western yew *(Taxus brevifolia)*, incense-cedar, Engelmann spruce *(Picea engelmannii)*, lodgepole pine, and subalpine fir *(Abies lasiocarpa)*. Other shrubs: Sadler oak, wood rose, and snowberry. Other herbs: queenscup.

Abies magnifica/Quercus vaccinifolia (California red fir/huckleberry oak) habitat type. Brewer spruce is an occasional minor climax species. Other trees: white fir, Douglas-fir, sugar pine, lodgepole pine, and western white pine. Other shrubs: greenleaf manzanita, pine mat manzanita, and bush chinkapin *(Castanopsis sempervirens)*.

- *Tsuga mertensiana* zone, Siskiyou Mountains

Tsuga mertensiana/Vaccinium membranaceum (mountain hemlock/thinleaf huckleberry) habitat type. Brewer spruce is a codominant climax species. Other trees: California red fir, western white pine, and Alaska-cedar *(Chamaecyparis nootkatensis)*.

- *Tsuga mertensiana* zone, central and eastern Klamath region

Tsuga mertensiana/Phyllodoce empetriformis (western hemlock/heather) habitat type. Brewer spruce is an occasional codominant climax species. Other trees: California red fir, white fir, western white pine, and lodgepole pine. Other shrubs: Labrador-tea *(Ledum glandulosum)*.

Tsuga mertensiana/Quercus vaccinifolia (western hemlock/huckleberry oak) habitat type. Brewer spruce is of minor importance as a climax species. Other trees: California red fir and western white pine. Other shrubs: pine mat manzanita, bush chinkapin, and greenleaf manzanita.

Brewer spruce is a minor component in three forest cover types *(4)*: Mountain Hemlock (Society of American Foresters Type 205), Red Fir (Type 207), and California Mixed Subalpine (Type 256).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Brewer spruce is monoecious. Strobilus buds form in early summer and develop in the fall. The dark purple male strobili are borne the following spring in axils of needles of the previous year's shoots, on branches throughout the tree. The pollen-bearing strobili are from 19 to 32 mm (0.75 to 1.25 in) long and about 13 mm (0.5 in) in diameter. Pollen is shed in early summer; the male strobili dry and fall soon after pollen is shed. Female strobili are borne at the tips of primary branches in the upper two-thirds of the crown. They develop into erect, dark green, cylindrical conelets that are 38 mm (1.5 in) long and 13 mm (0.5 in) thick when receptive. The female conelets are apparently receptive at the time pollen is shed. The location of female and male flowers throughout the tree, concurrent with timing of strobilus development, apparently encourages selfing of Brewer spruce located singly or in small, isolated stands. After pollination, the conelets turn down and mature the same season into dark brown cones 8 to 15 cm (3 to 6 in) long. The fruit matures from September to October; dissemination immediately follows.

Seed Production and Dissemination—Seed production starts when the trees are from 20 to 30 years old. Actual production has not been determined. Observations indicate that mature Brewer spruce trees are fair seed producers; crops occur at 2-year intervals, and some trees produce cones each year.

The seeds are 3 to 5 mm (0.1 to 0.2 in) long; the wing is four times as long as the seed. The seeds are the largest of the North American spruces: 134,500/kg (61,000/lb), with a range of 112,500 to 163,000/kg (51,000 to 74,000/lb). The relatively large wing aids dissemination of the seed by the wind. Cones and seeds do not appear to be a preferred food for rodents.

Seeds may be stored for 5 to 17 years in sealed containers at low temperatures, 1° to 3° C (33° to 38° F), at a moisture content of 4 to 8 percent. A cold, moist stratification of 30 days increases germination. Germination of sound seed ranges from 50 to 96 percent; the reported average is 88 percent *(15)*.

Seedling Development—The germination of Brewer spruce is epigeal, seedlings becoming established on all types of natural seedbeds: decaying logs, forest humus, loose soil from upturned roots, and leaf litter under brush fields. Throughout the range of Brewer spruce, natural regeneration is abundant under dense Brewer spruce-white fir stands. These stands contain an average of 1,360 Brewer spruce and 3,460 white fir seedlings per hectare (550 and 1,400/acre) less than 15 cm (6 in) in height. Brewer spruce seedlings cannot survive strong sunlight. The shallow, slow-growing root system causes the seedlings to be susceptible to the high moisture stress and temperatures of exposed sites. Brewer spruce seedlings are usually lacking in clearcuts, even when these are adjacent to stands containing large cone-bearing trees.

Seedlings are small, with four to seven cotyledons. Initial growth is slow; the epicotyl height growth is less than 6 mm (0.24 in) the first season.

Subsequent growth of seedlings is slow but quite variable. Under dense stands, the age of seedlings 1.37 m (4.5 ft) tall ranges from 27 to 82 years. Brewer spruce seedlings growing in south-facing montane chaparral were from 25 to 40 years old when they were 1.37 m (4.5 ft) tall. Small Brewer spruce survive overstory removal.

Vegetative Reproduction—Layering has not been observed in natural stands of Brewer spruce. Artificial propagation is best from seed *(10)*.

Sapling and Pole Stages to Maturity

Growth and Yield—After the seedling stage, height growth of Brewer spruce is slower than its common associates, Douglas-fir, white fir, red fir, and western white pine. In several stands in the Siskiyou Mountains, annual height growth of sapling and pole-size Brewer spruce averaged 0.15 m (0.5 ft).

Most mature stands of Brewer spruce consist of a wide range of ages and sizes. Numerous stands contain Brewer spruce up to 117 cm (46 in) in diameter, the largest 125 cm (49.3 in) in d.b.h. and 48.8 m (160 ft) in height. The biggest Brewer spruce listed by the American Forestry Association *(1)* has a circumference of 4.17 m (13.67 ft) at 1.37 m (4.5 ft) above the ground and is 51.8 m (170 ft) tall; it is located in the Siskiyou National Forest in southwest Oregon. The general structure of a mixed species, all-aged stand (Sadler oak habitat type) is shown in table 1.

Little volume or yield information is available for these Brewer spruce stands. The total basal area of the few stands sampled averages 47 m^2/ha (205 ft^2/acre), with a current annual increment of 2 m^2/ha (9 ft^2/acre) *(15)*.

Rooting Habit—Brewer spruce has a shallow root system on all soils; however, on deeper soils, a few vertical roots may extend several meters in depth.

Reaction to Competition—Brewer spruce is tolerant of shade at all ages and is very competitive. In the *Abies magnifica* zone on mesic to xeric sites, it is more competitive than mountain hemlock, Port-Orford-cedar, white fir, Douglas-fir, Alaska-cedar, incense-cedar, sugar pine, western white pine, ponderosa pine, lodgepole pine, and Jeffrey pine. California red fir is considered slightly more competitive on mesic sites because of its faster height growth and longer lifespan.

Brewer spruce is well adapted to growth at cool temperatures during the growing season. Its light compensation point is less than 2 percent of full sunlight. Brewer spruce can withstand considerable soil drought but is extremely sensitive to high evaporation demands. The stomata close under high evaporation, halting photosynthesis *(17)*.

Brewer spruce is best managed on mesic sites characterized by the presence of Sadler oak. It grows best in mixed-species stands with uneven-aged management.

Brewer spruce can be planted under montane chaparral dominated by Sadler oak, huckleberry oak, and greenleaf manzanita. It has the ability to grow well under competition for soil moisture and light.

Damaging Agents—The shallow root system of Brewer spruce makes it more susceptible than its associates to windthrow. In some areas, the high incidence of root rot *(Heterobasidion annosum)* further lowers its resistance to wind. Thin bark and long weeping branches make Brewer spruce susceptible to fire. Areas predictably occupied by Brewer spruce are limited to fire-resistant open forests on north-facing slopes or rocky ridges (fig. 3). A series of major forest fires in 1987 burned throughout the range of Brewer spruce. Most of the small, pure stands on north slopes were not damaged. In the more prevalent mixed stands, low-intensity ground fires killed the Brewer spruce and white fir, but the thick-barked Douglas-fir, pines, and California red fir survived. The recovery of Brewer spruce may take decades or centuries because of the extent of these fires. The increased potential of forest fires and inability of Brewer spruce seedlings to tolerate high moisture stress may result in its rapid extinction. If global warming occurs *(11)*, it could threaten the existence of localized tree species such as Brewer spruce.

Table 1—Stand structure of mixed species, all-aged Brewer spruce stands (Sadler oak habitat type)

Diameter class	Brewer spruce	White fir	Red fir	Douglas-fir	Western white pine	Sugar pine
cm				*trees/ha*		
3 to 29	430	506	82	69	—	—
30 to 59	114	32	27	2	7	—
60 to 89	17	15	15	—	2	—
90 to 119	2	—	7	—	—	—
120+	—	—	2	2	—	2
in				*trees/acre*		
1 to 11	174	205	33	28	—	—
12 to 23	46	13	11	1	3	—
24 to 35	7	6	6	—	1	—
35 to 47	1	—	3	—	—	—
47+	—	—	1	1	—	1

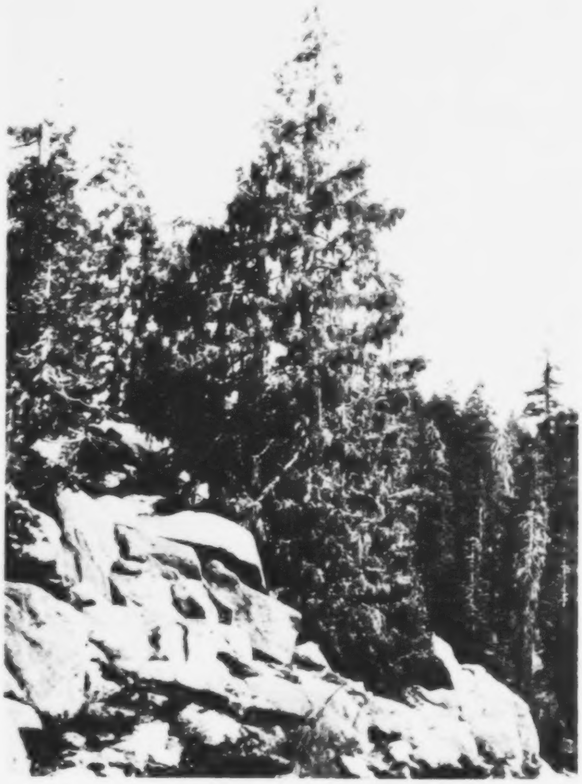

Figure 3—*Brewer spruce on the Klamath National Forest, CA.*

As a small tree, Brewer spruce has enough flexibility to bend under the weight of heavy snow. It develops a pistol butt as the tree matures.

Comparatively little damage from insects or fungi has been recorded for Brewer spruce *(3)*. The Cooley spruce gall adelgid *(Adelges cooleyi)* is common but does little damage *(6)*. Seed chalcids *(Megastigmus* spp.) have been observed in mature seeds. In some areas, 36 percent of the Brewer spruce was parasitized by the dwarfmistletoe *Arceuthobium*

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campylopodum (8). Brewer spruce is intolerant of industrial fumes.

Special Uses

The wood of Brewer spruce has no special uses. Harvested trees are normally mixed with other species and utilized as low grade lumber. In Europe, it has been considered one of the most popular of all ornamental conifers *(10)*.

Genetics

Little if any variability has been observed throughout the restricted range of Brewer spruce. In the eastern Klamath area, Brewer spruce grows adjacent to Engelmann spruce without hybridization *(12)*.

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Picea engelmannii Parry ex Engelm. **Engelmann spruce**

Pinaceae Pine family

Robert R. Alexander and Wayne D. Shepperd

Engelmann spruce is one of the seven species of spruce indigenous to the United States *(62)*. Other common names are Columbian spruce, mountain spruce, white spruce, silver spruce, and pino real.

Habitat

Native Range

Engelmann spruce is widely distributed in the western United States and two provinces in Canada *(61)*. Its range extends from British Columbia and Alberta, Canada, south through all western states to New Mexico and Arizona (fig. 1).

In the Pacific Northwest, Engelmann spruce grows along the east slope of the Coast Range from west central British Columbia, south along the crest and east slope of the Cascades through Washington and Oregon to northern California *(6,13,20)*. It is a minor component of these high-elevation forests.

Engelmann spruce is a major component of the high-elevation Rocky Mountain forests, growing in the Rocky Mountains of southwestern Alberta, south through the high mountains of eastern Washington and Oregon, Idaho, and western Montana to western and central Wyoming, and in the high mountains of southern Wyoming, Colorado, Utah, eastern Nevada, New Mexico, and northern Arizona *(6,13,20)*.

Climate

Engelmann spruce grows in a humid climate with long, cold winters and short, cool summers. It occupies one of the highest and coldest forest environments in the western United States, characterized by heavy snowfall and temperature extremes of more than −45.6° C (−50° F) to above 32.2° C (90° F). Climatic data for four subregions of the United States within the species range are given in table 1 *(23,42,65,100)*.

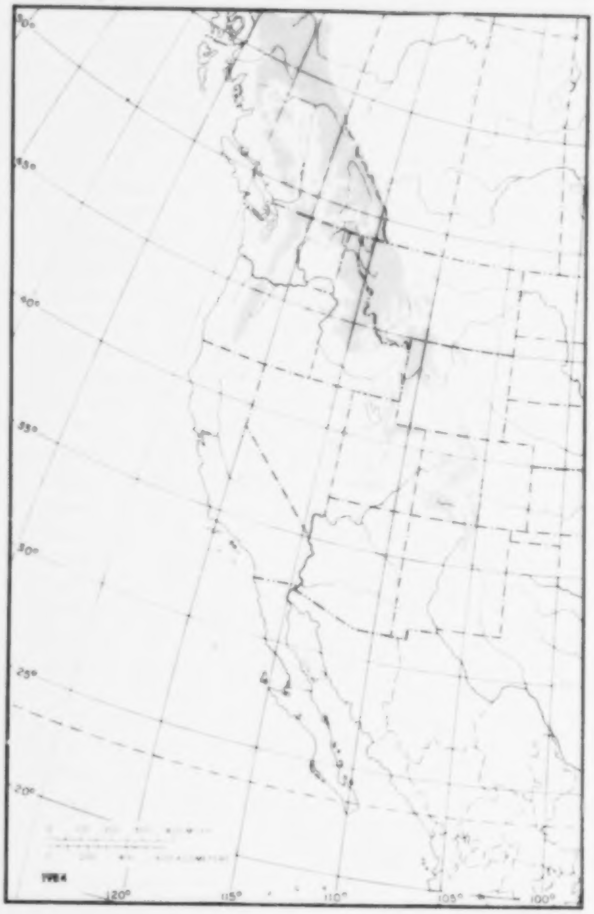

Figure 1—*Natural range of Engelmann spruce.*

The range of mean annual temperatures is narrow considering the wide distribution of the species. Average annual temperatures are near freezing, and frost can occur any month of the year. Average precipitation exceeds 61 cm (24 in) annually, with only moderate or no seasonal deficiency. Summer is the driest season in the Cascades and Rocky Mountains west of the Continental Divide south to southwestern Colorado. The mountains east of the divide, in southwestern Colorado, and in New Mexico and Arizona, receive considerable summer rainfall, while winter snowfall can be light *(23,48,64,100)*. Winds are predominantly from the west and southwest and can be highly destructive to Engelmann spruce *(13,20)*.

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Table 1.—Climatological data for four regional subdivisions within the range of Engelmann spruce

Location	Average temperature Annual		July		January		Annual precip.		Annual snowfall		Frost each period
	°C	°F	°C	°F	°C	°F	cm	in	cm	in	days
Pacific Northwest	2	35	10–13	50–55	–9 to –7	15–20	152–406	60–160	1015+	400+	45–90
U.S. Rocky Mountains											
Northern[1]	–1 to 2	30–35	4–13	45–55	–12 to –7	10–20	61–114	24–45+	635+	250+	[4]30–60
Central[2]	–1 to 2	30–35	10–13	50–55	–12 to –9	10–15	61–140	24–55	381–889+	150–350+	[4]30–60
Southern[3]	2	35	10–16	50–60	–9 to –7	15–20	61–89+	24–35+	508	200+	[4]30–75

[1] Includes the Rocky Mountains of Montana and Idaho and associated mountains of eastern Washington and Oregon.
[2] Includes the Rocky Mountains of Wyoming and Colorado and associated mountains of Utah.
[3] Includes the Rocky Mountains and associated ranges of New Mexico and Arizona and the plateaus of southern Utah.
[4] Frost may occur any month of the year.

Soils and Topography

Information on soils where Engelmann spruce grows is limited. In the Pacific Coast region, soil parent materials are mixed and varied. Country bedrock is composed of a variety of sedimentary, igneous, and metamorphic rock. The most common of the great soil groups are Cryorthods (Podzolic soils), Haplumbrepts (western Brown forest soils), Haplorthods (Brown Podzolic soils), Hapludalfs (Gray-Brown Podzolic soils), and Haploxerults and Haplohumults (Reddish-Brown Lateritic soils); these great soil groups developed from deep glacial and lacustrine deposits, deep residual material weathered in place from country rock, and volcanic lava and ash. Xerochrepts (Regosolic soils), developed from shallow residual material, are also widespread. Xeropsamments (Regosolic soils) and Haplaquolls (Humic Gley soils) are the principal soils derived from alluvium. On the east side of the Cascade crest, soils are largely Haploxeralfs (Non-Calcic Brown soils) and Haploxerolls (Chestnut soils) *(39,103)*.

In the Rocky Mountain subalpine zone, soil materials vary according to the character of the bedrock from which they originated. Crystalline granite rock predominates, but conglomerates, shales, sandstones, basalts, and andesites commonly occur. Glacial deposits and stream alluvial fans are also common along valley bottoms. Of the great soils group, Cryorthods (Podzolic Soils) and Haplorthods (Brown Podzolic Soils) occur extensively on all aspects. Cryochrepts (Thick Cold Soils) occur extensively on the drier aspects. Aquods (Ground-water Podzolic Soils) are found in the poorly drained areas. Cryoboralfs (Gray-Wooded Soils) are found where timber stands are less dense and parent material finer textured. Haploborolls (Brown Forest Soils) occur mostly in the lower subalpine zone along stream terraces and side slopes. Lithics (Lithosolic Soils) occur wherever bedrock is near the surface. Aquepts (Bog Soils) and Haplaquepts (Humic Gley Soils) occur extensively in poorly drained upper stream valleys *(48,103)*.

Regardless of the parent materials, spruce grows best on moderately deep, well drained, loamy sands and silts, and silt and clay loam soils developed from a variety of volcanic and sedimentary rock. Good growth also is made on glacial and alluvial soils developed from a wide range of parent materials, where an accessible water table is more important than physical properties of the soil. It does not grow well on rocky glacial till, heavy clay surface soils, saturated soils, or on shallow, dry coarse-textured sands and gravels developed primarily from granitic and schistic rock or course sandstones and conglomerates *(13,23)*.

Along the east slope of the Coast Range and interior valleys of southwestern British Columbia, Engelmann spruce grows at 762 to 1067 m (2,500 to 3,500 ft). Farther south in the Cascade Mountains of Washington and Oregon, it generally grows at 1219 to 1829 m (4,000 to 6,000 ft), but it may be found at 2438 m (8,000 ft) on sheltered slopes and at 610 m (2,000 ft) in cold pockets along streams and valley bottoms. In northern California, spruce grows at 1219 to 1524 m (4,000 to 5,000 ft) (16,98).

South of the Peace River Plateau in the Canadian Mountains of British Columbia and Alberta, Engelmann spruce grows at 762 to 1829 m (2,500 to 6,000 ft); in the Rocky Mountains of Idaho and Montana and in the adjacent mountains of eastern Washington and Oregon, at 610 to 2743 m (2,000 to 9,000 ft). But above 1829 to 2286 m (6,000 to 7,500 ft), it is a minor component of the stand, and below 1524 m (5,000 ft) it is confined to moist, low slopes and cold valley bottoms *(20)*.

Engelmann spruce is found at 2743 to 3353 m (9,000 to 11,000 ft) in the Rocky Mountains of Utah, Wyoming, and Colorado, but it may extend as low as 2438 m (8,000 ft) along cold stream bottoms and to timberline at 3505 m (11,500 ft). In the Rocky Mountains of New Mexico and Arizona and on the plateaus of southern Utah, it grows at 2896 to 3353 m (9,500 to 11,000 ft), but it may grow as low as 2438 m (8,000 ft) and as high as 3658 m (12,000 ft) *(13,20).*

Associated Forest Cover

Engelmann spruce most typically grows together with subalpine fir *(Abies lasiocarpa)* to form the Engelmann Spruce—Subalpine Fir (Type 206) forest cover type. It may also occur in pure or nearly pure stands. Spruce grows in 15 other forest types recognized by the Society of American Foresters, usually as a minor component or in frost pockets *(95):*

201	White Spruce
205	Mountain Hemlock
208	Whitebark Pine
209	Bristlecone Pine
210	Interior Douglas-Fir
212	Western Larch
213	Grand Fir
215	Western White Pine
216	Blue Spruce
217	Aspen
218	Lodgepole Pine
219	Limber Pine
224	Western Hemlock
226	Coastal True Fir–Hemlock
227	Western Redcedar–Western Hemlock

The composition of the forest in which Engelmann spruce grows is influenced by elevation, exposure, and latitude *(30).*[1] In the Rocky Mountains and Cascades, subalpine fir is its common associate at all elevations. In the northernmost part of its range along the Coast Range and in the Rocky Mountains of Canada, it mixes with white spruce *(Picea glauca),* black spruce *(Picea mariana),* Douglas-fir *(Pseudotsuga menziesii),* balsam poplar *(Populus balsamifera),* and paper birch *(Betula papyrifera).* In the Rocky Mountains of Montana and Idaho, in the Cascades, and in the mountains of eastern Washington and Oregon, associates at lower and middle elevations are western white pine *(Pinus monticola),* Douglas-fir, western larch *(Larix occidentalis),* grand fir *(Abies grandis),* and lodgepole pine *(Pinus contorta);* associates at higher elevations are Pacific silver fir *(Abies amabilis),* mountain hemlock *(Tsuga mertensiana),* alpine larch *(Larix lyallii),* and whitebark pine *(Pinus albicaulis).* In the Rocky Mountains south of Montana and Idaho, and in the mountains of Utah, lodgepole pine, interior Douglas-fir *(Pseudotsuga menziesii* var. *glauca),* blue spruce *(Picea pungens),* white-fir *(Abies concolor),* aspen *(Populus tremuloides),* and occasionally ponderosa pine *(Pinus ponderosa)* and southwestern white pine *(Pinus strobiformis),* are common associates at lower and middle elevations, and corkbark fir *(Abies lasiocarpa* var. *arizonica),* limber pine *(Pinus flexilis),* and bristlecone pine *(Pinus aristata)* at high elevations. Engelmann spruce extends to timberline in the Rocky Mountains south of Idaho and Montana, and may form pure stands at timberline in the southernmost part of its range. In the Canadian Rockies of southwestern Alberta and adjacent British Columbia and into the Rocky Mountains north of Wyoming and Utah, and the Cascades, spruce usually occupies moist sites below timberline; its high-elevation associates form timberline forests *(6,20).*

Rocky Mountain maple *(Acer glabrum)* (warm, moist sites); twinflower *(Linnaea borealis),* (cool, moist sites); common creeping juniper *(Juniperus communis)* (warm, dry sites); and grouse whortleberry *(Vaccinium scoparium),* heartleaf arnica *(Arnica cordifolia),* boxleaf myrtle *(Pachistima myrsinites),* elk sedge *(Carex geyeri),* mountain gooseberry *(Ribes montigenum),* and fireweed *(Epilobium angustifolium)* (cool, dry sites) occur as undergrowth throughout much of the range of Engelmann spruce. Undergrowth vegetation is more variable than tree associates, however. Undergrowth characteristically found in the Pacific Northwest Region and the Rocky Mountains and associated ranges north of Utah and Wyoming include: Labrador-tea *(Ledum glandulosum),* Cascades azalea *(Rhododendron albiflorum),* rusty skunkbrush *(Menziesia ferruginea),* woodrush *(Luzula hitchcockii),* dwarf huckleberry *(Vaccinium cespitosum),* and blue huckleberry *(Vaccinium globulare),* (cool, moist sites); false solomons-seal *(Smilacina stellata),* queenscup beadlily *(Clintonia uniflora),* twistedstalk *(Streptopus amplexifolius),* and sweetscented bedstraw *(Galium triflorum)* (warm, moist sites); pinegrass *(Calamagrostis rubescens)* and beargrass *(Xerophyllum tenax)* (cool, dry sites); Oregongrape *(Berberis repens),* white spirea *(Spiraea betulifolia),* and big whortleberry *(Vaccinium membranaceum)* (warm, dry sites); and marsh-marigold *(Caltha leptosepala),* devilsclub *(Oplopanax horridum),* and bluejoint reedgrass *(Calamagrostis canadensis)* (wet sites) *(14,39).*

Undergrowth characteristically found in the Rocky Mountains and associated ranges south of Idaho and

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[1] Classification of forest vegetation into "habitat types" based on methodology developed by Daubenmire *(31)* and Daubenmire and Daubenmire *(33)* and modified by others, is available for much of the western forest land. However, the classification has not been completed for all land where Engelmann spruce grows. Moreover, because of the great number of these habitat types and the complexity of their descriptions, they have not been included in this paper.

Montana include: mountain bluebells *(Mertensia ciliata)* and heartleaf bittercress *(Cardamine cordifolia)* (cool, moist sites); thimbleberry *(Rubus parviflorus)* (warm, moist sites); red buffaloberry *(Shepherdia canadensis)*, Oregongrape, mountain snowberry *(Symphoricarpos oreophilus)*, and Arizona peavine *(Lathyrus arizonicus)* (warm, dry sites); and Rocky Mountain whortleberry *(Vaccinium myrtillus)*, groundsel *(Senecio sanguiosboides)*, polemonium *(Polemonium delicatum)*, daisy fleabane *(Erigeron eximius)*, prickly currant *(Ribes lacustre)*, sidebells pyrola *(Pyrola secunda)*, and mosses (cool, dry sites) *(14)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Engelmann spruce is monoecious; male and female strobili are formed in the axils of needles of the previous year's shoots after dormancy is broken, usually in late April to early May. Ovulate strobili (new conelets) are usually borne near ends of the shoots in the upper crown and staminate strobili on branchlets in the lower crown *(38,102)*. Separation of male and female strobili within the crown reduces self-fertilization. The dark purple male flowers are ovoid to cylindrical and pendant. Female flowers are scarlet, erect, and cylindrical. Male flowers ripen and pollen is wind disseminated in late May and early June at low elevations, and from mid-June to early July at high elevations. The conelets grow rapidly and soon reach the size of the old cones that may have persisted from previous years. The new cones mature in one season and are 2.5 to 6.3 cm (1 to 2.5 in) long. They ripen in August to early September, open, and shed their seed. The cones may fall during the following winter or may remain attached to the tree for some time *(20, 89,102)*.

Seed Production and Dissemination—Although open-grown Engelmann spruces begin bearing cones when they are 1.2 to 1.5 m (4 to 5 ft) tall and 15 to 40 years old, seed production does not become significant until trees are larger and older. The most abundant crops in natural stands are produced on healthy, vigorous, dominant trees 3.8 dm (15 in) or more in diameter at breast height and 150 to 250 years old. Engelmann spruce is a moderate to good seed producer *(11,19,21)*. Good to bumper seed crops, based on the following criteria, are generally borne every 2 to 5 years, with some seed produced almost every year *(19)*:

Number of sound seeds/hectare		Seed crop rating
0–24,700	(0–10,000/acre)	Failure
24,700–123,500	(10,000–50,000/acre)	Poor
123,500–247,000	(50,000–100,000/acre)	Fair
247,000–617,500	(100,000–250,000/acre)	Good
617,500–1,235,000	(250,000–500,000/acre)	Heavy
>1,235,000	(>500,000/acre)	Bumper

There is great variation in seed production from year to year and from area to area. In one study on the Fraser Experimental Forest in Colorado, annual seed production averaged only 32,100 sound seeds per acre during the period 1956–65 *(4)*. Only one good and two moderate crops were recorded. In more recent studies, spruce seed production has been greater, possibly because the studies were better designed to sample seed production. One such study of seed production on five National Forests, covering 42 area-seed crop years from 1962 to 1971, rated seed crops as 5 bumper, 1 heavy, 6 good, and the remaining 30 fair to failure *(74)*. In the one year, 1967, that a bumper seed crop was produced on all areas, seed production was the highest ever recorded in Colorado *(84)*. In another study on the Fraser Experimental Forest covering 15 years (1970–84) and 13 locations, seed production was rated 2 bumper, 3 heavy, 2 good and 8 fair to failure *(21)*.

In the northern Rocky Mountains, Boe *(26)* analyzed cone crops in Montana between the years 1908 and 1953. Twenty-two crops observed west of the Continental Divide during the 45-year period were rated: 5 good, 8 fair, and 9 poor. East of the Divide, seed production was poorer: only 2 good, 4 fair, and 15 poor crops were reported for a 21-year period. In other studies in the Northern and Intermountain Regions, seed production was rated as good to bumper in 1 year out of 5, with the other 4 years rated as failures *(78,96)*.

Observations in spruce forests before seedfall have indicated that part of each seed crop is lost to cone and seed insects *(13)*. In a recently completed study in Colorado, insect-caused loss of Engelmann spruce seed averaged 28 percent of the total seed produced during a 4-year period (1974–1977) *(88)*. The percentage of infested cones was highest during years of poor seed production. The primary seed-eating insects were a spruce seedworm *(Cydia youngana = (Laspeyresia youngana)* and an unidentified species of fly, possibly a *Hylemya*, found only in the larval stage.

Some seed is lost from cutting and storing of cones by pine squirrels *(Tamiasciurus hudsonicus fremonti)*, but the actual amount is unknown. After seed is shed, small mammals such as deer mice *(Peromyscus maniculatus)*, red-backed mice *(Clethrionomys gapperi)*, mountain voles *(Microtus montanus)*, and chipmunks *(Eutamias minimus)* are the principal source of seed loss. Undoubtedly, mammals consume much seed, but the amount is not known and results of studies on protecting seed are conflicting. For example, in western Montana, spruce seedling success was little better on protected than unprotected seed spots *(90)*, but in British Columbia, protection of spruce seed from rodents was essential to spruce regeneration success *(94)*.

Cones begin to open in September. Most seed is shed by the end of October, but some falls throughout the winter. The small, winged seeds are light, averaging about 297,000/kg (135,000/lb) *(102)*. Nearly all of the seed is disseminated by the wind; squirrels, other mammals, and birds are not important in seed dispersal.

Seed is dispersed long distances only in years of bumper seed crops. For example, studies in the Rocky Mountains show that 237,200 to 617,800 sound seeds/ha (96,000 to 250,000/acre) were dispersed 122 to 183 m (400 to 600 ft) from the source into clearcut blocks 183 m to 244 m (600 to 800 ft) wide (74). Seedfall in cut stands ranged from 1,236,000 to 12,355,000 seeds/ha (500,000 to 5,000,000/acre). In years of good to heavy seed crops, seedfall into cleared openings diminished rapidly as distance from seed source increased. Prevailing winds influence the pattern of seedfall in openings 61 to 244 m (200 to 800 ft) across, with about 40 percent of the seeds falling within 31 m (100 ft) of the windward timber edge *(4,16,74)*. Seedfall then diminishes but at a less rapid rate of decline as distance increases to about two-thirds of the way—46 to 183 m (150 to 600 ft)—across the openings. At that distance, the average number of seeds falling is about 25 percent (at 46 m [150 ft]) to less than 5 percent (at 183 m [600 ft]) of the number of released in the uncut stand *(4,74,78,80)*. Beyond this point, seedfall gradually increases toward the leeward timber edge, but is only about 30 percent of the seedfall along the windward edge *(73,16)*. In the openings observed, a U-shaped pattern of seedfall was poorly defined. The "tailing-off" suggests that significant quantities of seed were released during periods of high winds *(36)*.

Seedling Development—Viability of Engelmann spruce seed is rated good and the vitality persistent. The average germinative capacity of spruce is higher than for many associated species *(102)*:

Species	Average germinative capacity
Engelmann spruce	69
Subalpine fir	31–34
Lodgepole pine	65–80
Western white pine	44
Interior Douglas-fir	60–93
Western larch	57
Grand fir	46–57
Western hemlock	53–56
Pacific silver fir	20–26
White fir	30–37

Viable seeds of spruce that survive over winter normally germinate following snowmelt when seedbeds are moist and air temperature is at least 7° C (45° F). Field germination of spruce over long periods in Colorado have ranged from 0 to 28 percent of the sound seeds dispersed, depending upon the seedbed and environmental factors *(9,73)*.

In the undisturbed forest, spruce seeds germinate and seedlings become established on duff, litter, partially decomposed humus, decaying wood, and mounds of mineral soil upturned by windthrown trees. Any disturbance that removes the overstory produces new microhabitats *(80)*. Under these circumstances, germination and initial establishment are generally better on prepared mineral soil, and disturbed mineral soil and humus seedbeds because moisture conditions are more stable *(27,35,41,73,94)*. However, initial survival of spruce on severe sites at high elevations in the Intermountain Region was higher on duff seedbeds than on mineral soil seedbeds *(37)*. Spruce seedling establishment on burned seedbeds has been variable. Success is related to severity of burn, depth of ash, and amount of exposed mineral soil *(29,80,91)*. Regardless of the seedbed, high initial mortality usually slows establishment of seedlings. Once established (at least 5 years old), the ability to survive is not increased by a mineral soil seedbed, but is favored by adequate soil moisture, cool temperature, and shade.

Engelmann spruce will germinate in all light intensities found in nature, but 40 to 60 percent of full shade is most favorable for seedling establishment at high elevations. Light intensity and solar radiation are high at elevations and latitudes where spruce grows in the central and southern Rocky Mountains, and seedlings do not establish readily in the open. Planted seedlings often develop a chlorotic appearance that has been attributed to solarization—a phenomenon by which light intensity inhibits photosynthesis and which ultimately results in death *(82)*. Mortality can be reduced by shading seedlings. At low elevations and high latitudes in the northern Rocky Mountains, spruce can become established and survive in the open *(17)*. Spruce can establish and survive better in low light intensities than its common, intolerant associates such as lodgepole pine, Rocky Mountain Douglas-fir, and aspen, but at extremely low light intensities it cannot compete favorably with such shade-enduring associates as the true firs and hemlocks *(20)*.

Engelmann spruce is restricted to cold, humid habitats because of its low tolerance to high temperature and drought *(25,45)*. However, solar radiation at high elevations heats soil surfaces [up to 66° C (150° F or more)] and increases water losses from both seedlings and soil by transpiration and evaporation *(9,73,80)*.

Because of its slow initial root penetration and extreme sensitivity to heat in the succulent stage, drought and heat girdling kill many first-year spruce seedlings. Drought losses can continue to be significant during the first 5 years of seedling development, especially during prolonged summer dry periods *(9,34,73)*.

Tree seedlings in the succulent stage are particularly susceptible to stem-girdling. The cortex is killed by a temperature of 54° C (130° F), but prolonged exposures to somewhat lower temperatures may also be lethal. On the Fraser Experimental Forest, heat-girdling caused much early seedling mortality on unshaded seedbeds *(9,73)*. Soil-surface temperature exceeded 65° C (150° F) in the open on a north aspect and 71° C (160° F) on a south aspect at 3200 m (10,500 ft) elevation in June. Maximum air temperature during this period did not exceed 26° C (78° F). In western Montana, at low elevations, soil surface temperatures exceeded 71° C (160° F) on gentle north slopes several times during one summer *(80)*. Early shade protection increased survival of newly germinated spruce seedlings; 30 to 50 percent of the seedlings were lost to heat-girdling on unshaded plots, compared to 10 percent on shaded plots. In southwestern Alberta, when newly germinated spruce seedlings were deprived of water, nearly three-fourths of the mortality on four different unshaded seedbed types was caused by heat-girdling *(34)*. Surface temperatures as low as 45° C (113° F) caused heat girdling, but losses were not high until soil surface temperatures were above 50° C (122° F). Shading reduced heat-girdling on all seedbed types. Soil surface temperatures in excess of lethal levels for spruce seedlings, especially on burned seedbeds, have been reported in British Columbia *(94)*.

Air and soil temperatures (below the surface) are not usually directly responsible for seedling mortality, but they affect growth. In a growth chamber study of Engelmann spruce seedlings under 30 different combinations of day and night temperatures, the greatest height and root growth, and top and root dry matter production was with a diurnal variation of 19° C (66° F) (air and soil) day temperatures and 23° C (73° F) (air and soil) night temperatures *(45)*. Shepperd *(92)*, using the same night temperature regime, raised the day soil temperature to 23° C (72° F) and significantly increased root growth.

Frost can occur any month of the growing season where spruce grows. It is most likely to occur in depressions and cleared openings because of cold air drainage and radiation cooling. Newly germinated spruce seedlings are most susceptible to early fall frosts. In a greenhouse and laboratory study, new seedlings did not survive temperatures as low as −9.5° C (15° F) until about 10 weeks old *(71)*. Terminal bud formation began at 8 weeks; buds were set and needles were mature at 10 to 12 weeks after germination.

After the first year, seedlings are most susceptible to frost early in the growing season when tissues are succulent. Shoots are killed or injured by mechanical damage resulting from tissue freezing and thawing. Frost damage has been recorded in most years in Colorado *(81)*. In light frost years, damage was minor, but heavy frosts either damaged or killed all new shoots of open-grown seedlings.

In early fall, the combination of warm daytime temperatures, nighttime temperatures below freezing, and saturated soil unprotected by snow are conducive to frost-heaving. On the Fraser Experimental Forest, Colorado, these conditions generally occurred about 1 out of 2 years *(9,73)*. Frost-heaving has been one of the principal causes of first-year seedling mortality on scarified seedbeds on north aspects *(9)*. Furthermore, seedlings continue to frost-heave after four growing seasons. Shading has reduced losses by reducing radiation cooling.

The moisture condition of the seedbed during the growing season largely determines first-year seedling survival. On some sites in the central Rocky Mountains, summer drought causes great first-year mortality, especially in years when precipitation is low or irregular. On the Fraser Experimental Forest in the central Rocky Mountains, drought and desiccation caused more than half the first-year seedling mortality on south aspects, and nearly two-thirds of the total after 5 years. On north aspects during the same period, drought accounted for about 40 percent of first-year seedling mortality, and more than half the mortality at the end of 5 years *(9)*.

In the northern Rocky Mountains, late spring and early summer drought is a serious threat most years to first-year seedlings. In western Montana, all seedlings on one area were killed by drought in a 2-week period in late summer when their rate of root penetration could not keep pace with soil drying during a prolonged dry period *(80)*. Late spring and early summer drought is also a serious cause of first-year seedling mortality in the southern Rockies. Drought losses can continue to be significant throughout the Rocky Mountains during the first 5 years of seedling development, especially during prolonged summer dry periods *(9,73)*.

The moisture provided by precipitation during the growing season is particularly critical to seedling survival during the first year. A greenhouse study of the effects of amount and distribution of moisture on seedling survival (simulating common summer precipitation patterns in north-central Colorado) showed that under favorable seedbed and environmental conditions: (1) at least 2.5 cm (1 inch) of well distributed precipitation is needed monthly before seedlings will survive drought; (2) with this precipitation pattern, more than 3.75 cm (1.5 in) of monthly rainfall is not likely to increase seedling survival; but (3) few seedlings will survive drought with less than 5 cm (2 in) of rainfall monthly when precipitation comes in only one or two storms *(18).*

Summer precipitation may not always benefit seedling survival and establishment. Summer storms in the Rocky Mountains may be so intense that much of the moisture runs off, especially from bare soil. Moreover, soil movement on unprotected seedbeds buries some seedlings and uncovers others *(80).*

Understory vegetation can be either a benefit or serious constraint to spruce seedling establishment *(2,35,83).* Spruce seedlings become established more readily on sites protected by willows *(Salix* spp.), shrubby cinquefoil *(Potentilla fruiticosa),* fireweed, and dwarf whortleberry than in the open. Because these plants compete less aggressively for available soil moisture than those listed below, the net effect of their shade is beneficial to seedling survival. In contrast, mortality occurs when spruce seedlings start near clumps of grass or sedges or scattered herbaceous plants such as mountain bluebells, currants *(Ribes* spp.), and Oregongrape that compete severely for moisture and smother seedlings with cured vegetation when compacted by snow cover *(83).*

The only significant biotic factor affecting spruce regeneration on a long-term study on the Fraser Experimental Forest was birds. About 15 percent to 20 percent of the total mortality resulted from the clipping of cotyledons on newly germinated seedlings by grey-headed juncos *(Junco caniceps) (9,73,75).*

Damping-off, needlecast, snowmold, insects, rodents, and trampling and browsing by large animals also kill spruce seedlings, but losses are no greater than for any other species *(20).*

The number of seeds required to produce a first-year seedling and an established seedling (5 years old) and the number of first-year seedlings that produce an established seedling vary greatly, depending upon seed production, distance from source, seedbed, and other environmental conditions. In one study in clearcut openings in Colorado during the period 1961–1975, covering a wide variety of conditions, on the average 665 sound seeds (range 60–2,066) were required to produce one first-year seedling, and 6,800 (range 926–20,809) to produce a seedling 4 or more years old. An average of 21 first-year seedlings was necessary to produce a single seedling 4 or more years old, although as few as 4 and as many as 24 first-year seedlings survived under different conditions *(74).*

Aspect and cultural treatments can also affect establishment of Engelmann spruce. In another Colorado study (covering the period 1969–1982), an average of 18 sound seeds was required to produce a single first-year seedling on shaded, mineral soil seedbeds on a north aspect; and 32 sound seeds were needed to produce a 5-year-old seedling. In contrast, 156 seeds were required to produce a first-year seedling on shaded, mineral soil seedbeds on a south aspect, and 341 seeds to produce a 5-year-old seedling *(8,9).* Shearer *(91),* studying the effects of prescribed burning and wildfire after clearcutting on regeneration in the western larch type in Montana, also found that natural and planted spruce survived better on the north aspect than on the south aspect.

Environmental conditions favorable and unfavorable to the establishment of Engelmann spruce natural regeneration are summarized in Figure 2.

The early growth of Engelmann spruce at high elevations is slow *(60).* First-year spruce seedlings field-grown on mineral soil seedbeds under partial shade in Colorado have a rooting depth of 7.6 to 10.2 cm (3 to 4 in), with a total root length of 12.7 cm (5 in) *(72).* In the Rocky Mountains of Arizona and New Mexico, root depths of vigorous 1-year-old seedlings averaged about 7.1 cm (2.8 in) on both shaded mineral soil seedbeds and on seedbeds where humus depth was about 2.5 cm (1 in) *(49).* Observations in the Rocky Mountains of Idaho and Montana and British Columbia indicate that first-year penetration of spruce seedlings averages only about 3.8 cm (1.5 in) *(80,94).*

Initial shoot growth of natural seedlings is equally slow in Colorado. First-year spruce seedlings are seldom taller than 2.5 cm (1 in). After 5 years, seedlings average 2.5 to 7.6 cm (1 to 3 in) in height under natural conditions, and 5.1 to 10.2 cm (2 to 4 in) in height on both partially shaded and unshaded, prepared, mineral-soil seedbeds. Seedlings 10 years old may be only 15.2 to 20.3 cm (6 to 8 in) tall under natural conditions, and 25.7 to 30.5 cm (10 to 12 in) tall on both partially shaded and unshaded, prepared, mineral-soil seedbeds *(7),* (fig. 3). After 10 years, trees grow faster, averaging about 1.2 to 1.5 m (4 to 5 ft) in height in about 20 years in full sun or light overstory shade and in about 40 years under moderate overstory shade. Severe suppression of seedlings does occur at low light levels. It is not uncommon to find trees 80 to 120 years old only 1.0 to 1.5 m (3 to 5 ft) tall under the heavy shade of a closed forest canopy *(76)* (fig. 4).

	Favorable	***Unfavorable***
Seed crop	More than 600,000 seeds per hectare (242,800/acre)	Less than 60,000 seeds per hectare (24,300/acre)
Aspect	North	South
Temperatures	Ambient air more than 0° C (32° F) night and less than 25° C (77° F) day; maximum surface less than 30° C (86° F)	Ambient air less than 0° C (32° F) night and more than 25° C (77° F) day; maximum surface greater than 30° C (86° F)
Precipitation	More than 10 mm (0.4 in)/week	Less than 10 mm (0.4 in)/week
Soil	Light-textured, sandy-loam	Heavy-textured, clay-loam
Seedbed	50 percent exposed mineral soil 40 to 60 percent dead shade Duff and litter less than 5 cm (2 in) Light vegetative cover	10 percent or less exposed mineral soil 10 percent or less dead shade Duff and litter more than 5 cm (2 in) Heavy vegetative cover
Survival	Seedlings more than 12 weeks old by mid-September Low population of birds and rodents that eat seeds and seedlings Protection from trampling Snow cover when frost-heaving conditions exist	Seedlings less than 12 weeks old by mid-September High population of birds and rodents that eat seeds and seedlings No protection from trampling No snow cover when frost-heaving conditions exist

Figure 2—*Environmental conditions favorable and unfavorable to Engelmann spruce regeneration* (9).

Seedling growth has been somewhat better elsewhere in the Rocky Mountains, especially at low elevations and high latitudes. For example, in one study in the intermountain West, annual shoot growth of natural 10-year-old seedlings averaged 11.4 cm (4.5 in) on clearcut areas, and 8.3 cm (3.2 in) on areas with a partial overstory *(67)*. Planted spruces, 5- to 8-years old, averaged 51 to 61 cm (20 to 24 in) in height in Utah. In Montana, planted spruces have been reported to reach breast height [1.4 m (4.5 ft)] in about 10 years *(21)*.

Early diameter growth of Engelmann spruce is less affected by competition for growing space than that of its more intolerant associates. In a study of seed spot density in northern Idaho, diameter growth of spruce seedlings after 17 years was only slightly greater on thinned seed spots, and height growth was unaffected by the thinning. In contrast, diameter and height growth of western white pine increased significantly as the number of seedlings per seed spot decreased *(79)*.

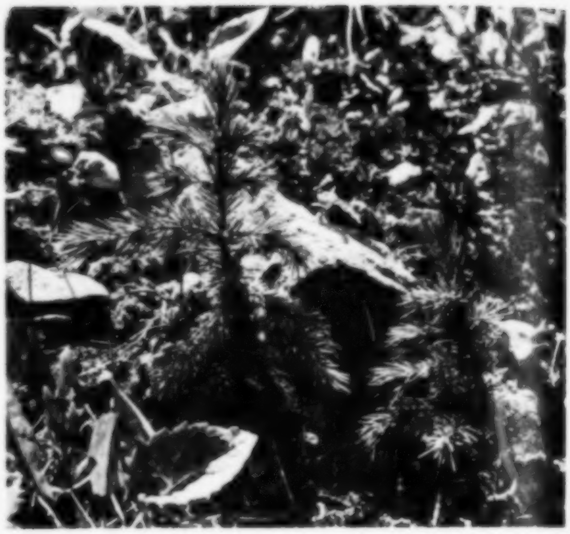

Figure 3—*Engelmann spruce seedlings on mineral soil seedbeds average only 20.3 cm to 30.5 cm (8 to 12 in) in height after 10 years.*

Vegetative Reproduction—Engelmann spruce can reproduce by layering *(47)*. It most often layers near timberline, where the species assumes a dwarfed or prostrate form. Layering can also occur when only a few trees survive fires or other catastrophes. Once these survivors have increased to the point where their numbers alter the microenvironment enough to improve germination and establishment, layering diminishes. In general, this form of reproduction is insignificant in the establishment and maintenance of closed forest stands *(21,76)*.

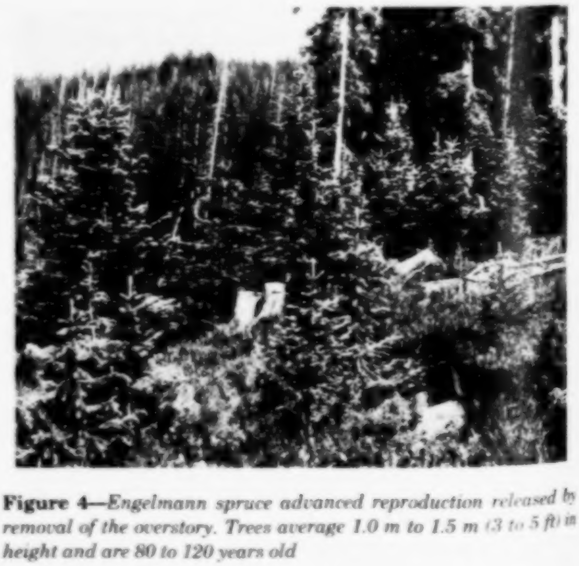

Figure 4—*Engelmann spruce advanced reproduction released by removal of the overstory. Trees average 1.0 m to 1.5 m (3 to 5 ft) in height and are 80 to 120 years old*

Sapling and Pole Stage to Maturity

Growth and Yield—Engelmann spruce is one of the largest of the high-mountain species. Under favorable conditions, average stand diameter will vary from 38.1 to 76.2 cm (15 to 30 in), and average dominant height from 14 to 40 m (45 to 130 ft), depending upon site quality and density *(20)* (fig. 5). Individual trees may exceed 101.6 cm (40 in) in diameter and 49 m (160 ft) in height *(60)*. Engelmann spruce is a long-lived tree, maturing in about 300 years. Dominant spruces are often 250 to 450 years old, and trees 500 to 600 years old are not uncommon *(13)*.

Engelmann spruce has the capacity to grow well at advanced ages. If given sufficient growing space, it will continue to grow steadily in diameter for 300 years, long after the growth of most associated tree species slows down *(20,60)*.

Yields are usually expressed for the total stand. Engelmann spruce does not normally grow in pure stands but in various mixtures with associated species. Average volume per hectare in old-growth (normally 250 to 350 years old) spruce-fir may be practically nothing at timberline, 12,350 to 37,070 fbm/ha (5,000 to 15,000 fbm/acre) on poor sites, and 61,780 to 98,840 fbm/ha (25,000 to 40,000 fbm/acre) on better sites. Volumes as high as 197,680 to 247,100 fbm/ha (80,000 to 100,000 fbm/acre) have been reported for very old stands on exceptional sites *(77,99)*. Average annual growth in virgin spruce-fir forests will vary from a net loss due to mortality to as much as 494 fbm/ha (200 fbm/acre), depending upon age, density, and vigor of the stand *(69)*. Engelmann spruce usually makes up at least 70 percent and often more than 90 percent of the basal area in trees 12.7 cm (5.0 in) and larger at breast height in these stands *(76)*.

With prompt restocking after timber harvest and periodic thinning to control stand density and maintain growth rates, growth of individual spruce trees and yields of spruce-fir stands can be greatly increased and the time required to produce the above volumes and sizes reduced. For example, in stands managed at the growing stock levels (GSL) considered optimum for timber production (GSL 140 to 180) on 140- to 160-year rotations with a 20-year thinning interval, average volumes per hectare will range from 74,100 to 98,800 fbm/ha (30,000 to 40,000 fbm/acre) on poor sites to 222,400 to 259,500 fbm 1 ha (90,000 to 105,000 fbm/acre) on good sites. Volume production declines on all sites when growing stock level is reduced below the optimum for timber production, and the decline is greater with each successive reduction in GSL. Average annual growth will vary from 445 to 1,606 fbm/ha (180 to 650 fbm/acre) *(15)*. Moreover, since most subalpine fir will be removed in early thinnings, these yields will be largely from Engelmann spruce.

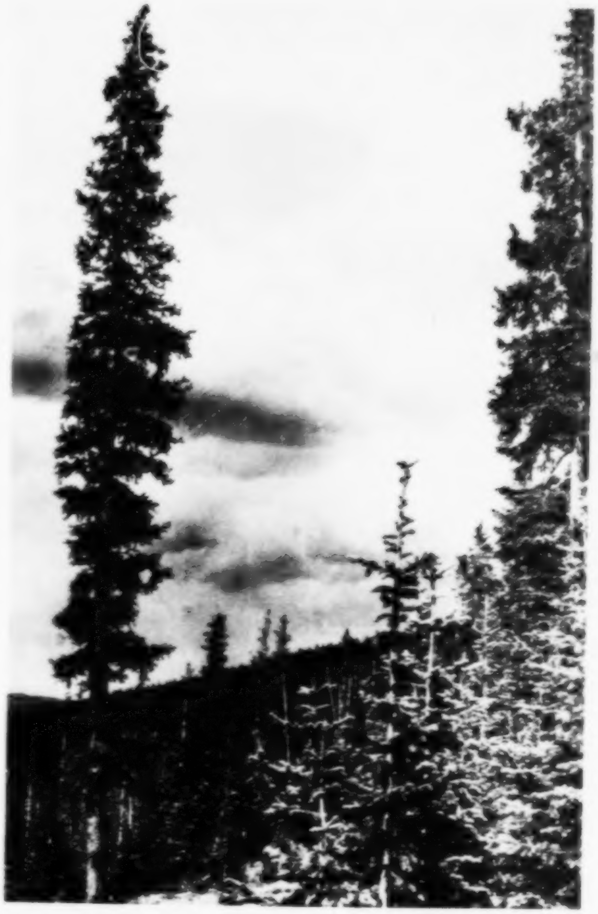

Figure 5—*Dominant Engelmann spruce on the Fraser Experimental Forest, Colorado. Tree at the left is 4.6 dm (18 in) in diameter, more than 27 m (90 ft) tall, and 250 years old at breast height.*

Rooting Habit—Engelmann spruce has a shallow root system. The weak taproot of seedlings does not persist beyond the juvenile stage, and when trees grow where the water table is near the surface or on soils underlain by impervious rock or clay hardpans, the weak, superficial lateral root system common to the seedling stage may persist to old age. Under these conditions, most roots are in the first 30 to 46 cm (12 to 18 in) of soil. But, where spruce grows on deep, porous, well drained soils, the lateral root system may penetrate to a depth of 2.4 m (8 ft) or more *(20)*.

Reaction to Competition—Engelmann spruce is rated tolerant in its ability to endure shade *(24)*. It is definitely more shade-enduring than interior Douglas-fir, western white pine, lodgepole pine, aspen, western larch, or ponderosa pine but less so than subalpine fir (the most common associate throughout much of its range), grand fir, white fir, and mountain hemlock. The Engelmann spruce—subalpine fir type is either a co-climax type or long-lived seral forest vegetation throughout much of its range. In the Rocky Mountains of British Columbia and Alberta, and south of Montana and Idaho, Engelmann spruce and subalpine fir occur as either codominants or in nearly pure stands of one or the other. In the Rocky Mountains of Montana and Idaho, and in the mountains of Utah, eastern Oregon and Washington, subalpine fir is the major climax species. Engelmann spruce may also occur as a major climax species, but more often it is a persistent long-lived seral species. Pure stands of either species can be found, however *(6)*.

Although spruce-fir forests form climax or near climax vegetation associations, they differ from most climax forests in that many stands are not truly all-aged *(60)*. Some stands are clearly single-storied, indicating that desirable spruce forests can be grown under even-aged management. Other stands are two- or three-storied, and multi-storied stands are not uncommon *(13,68)*. These may be the result of either past disturbances, such as fire, insect epidemics, or cutting, or the gradual deterioration of old-growth stands due to normal mortality from wind, insects, and disease. The latter is especially evident in the formation of some multi-storied stands. On the other hand, some multi-storied stands appear to have originated as uneven-aged stands and are successfully perpetuating this age-class structure *(10,43,104)*.

Although climax forests are not easily displaced by other vegetation, fire, logging, and insects have played an important part in the succession and composition of spruce-fir forests. Complete removal of the stand by fire or logging results in such drastic environmental changes that spruce and fir are usually replaced by lodgepole pine, aspen, or shrub and grass communities *(80,97)*. The kind of vegetation initially occupying the site usually determines the length of time it takes to return to a spruce-fir forest. It may vary from a few years, if the site is initially occupied by lodgepole pine or aspen, to as many as 300 years, if grass is the replacement community.

What is known about the utilization of water by Engelmann spruce in Colorado can be summarized as follows: (1) leaf water potential decreases in proportion to the transpiration rate but is influenced by soil temperature and water supply; (2) needle water vapor conductance (directly proportional to stomatal opening) is controlled primarily by visible irradiance and absolute humidity difference from needle to air (evaporative demand), with secondary effects from temperature and water stress; (3) nighttime minimum temperatures below 3.9° C (39° F) retard stomatal opening the next day, but stomata function well from early spring to late fall, and high transpiration rates occur even with snowpack on the ground; (4) leaf water vapor conductance is higher in Engelmann spruce than in subalpine fir, but lower than in lodgepole pine and aspen; (5) Engelmann spruce trees have less total needle area per unit area of sapwood water conducting tissue than subalpine fir but more than lodgepole pine and aspen; and (6) Engelmann spruce trees have a greater needle area per unit of bole or stand basal area than subalpine fir, lodgepole pine, and aspen. At equal basal area, annual canopy transpiration of spruce is about 80 percent greater than lodgepole pine, 50 percent greater than subalpine fir, and 220 percent greater than aspen. These high rates of transpiration cause Engelmann spruce to occur primarily on moist sites *(50,51,52,53,54,55,56,57,58)*.

Both even- and uneven-aged silvicultural systems are appropriate for use in Engelmann spruce forests, but not all cutting methods meet specific management objectives *(5,12,17)*. The even-aged cutting methods include clearcutting, which removes all trees in strips, patches, blocks, or stands with a single cut; and shelterwood cutting, which removes trees in one, two, or three cuts and its modifications. Because of susceptibility to windthrow, the seed-tree method is not a suitable way to regenerate spruce. The seedbed is prepared for regeneration after clearcutting, or after the seed cut with shelterwood cutting, by various methods ranging from burning and mechanical scarification to only that associated with logging activity *(5,12,17)*.

The uneven-aged cutting methods appropriate to spruce are individual tree and group selection cuttings and their modifications, which remove selected trees in all size classes at periodic intervals over the entire area or in groups up to 0.8 hectares (2 acres) in size. Reproduction occurs continuously, but methods of site preparation are limited *(12,13)*.

Shelterwood and individual tree selection cutting methods will favor associated species such as true firs and hemlocks over spruce. Clearcutting, group shelterwood, and group selection cutting methods will favor Engelmann spruce over these more tolerant associates, but will increase the proportion of intolerant associates such as lodgepole pine and Douglas-fir *(13)*.

Damaging Agents—Engelmann spruce is susceptible to windthrow, especially after any initial cutting in old-growth forests (fig. 6).

Partial cutting increases the risk because the entire stand is opened up and therefore vulnerable. Windfall is usually less around clearcuts because only the boundaries between cut and leave areas are vulnerable, but losses can be great if no special effort is made to locate windfirm cutting-unit boundaries *(1,3)*. While the tendency of spruce to windthrow is usually attributed to a shallow root system, the development of the root system varies with soil and stand conditions. Trees that have developed together in dense stands over long periods of time mutually protect each other and do not have the roots, boles, or crowns to withstand sudden exposure to wind if opened up too drastically. If the roots and boles are defective, the risk of windthrow is increased. Furthermore, regardless of kind or intensity of cutting, or soil and stand conditions, windthrow is greater on some exposures than others. Alexander *(13)* has identified spruce windfall risk in relation to exposures in Colorado as follows:

Below Average:

1. Valley bottoms, except where parallel to the direction of prevailing winds, and flat areas.
2. All lower, and gentle, middle north-east-facing slopes.
3. All lower, and gentle, middle south- and west-facing slopes that are protected from the wind by higher ground not far to windward.

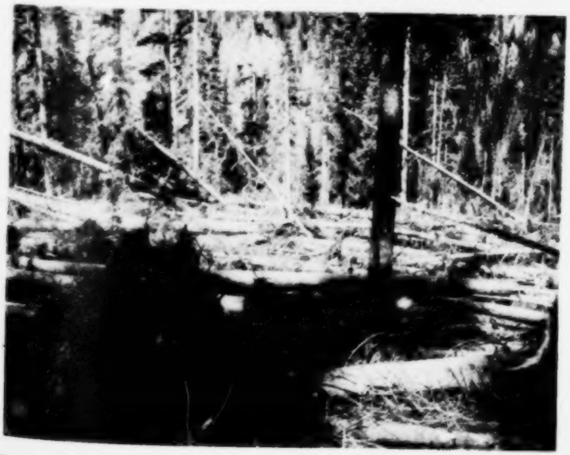

Figure 6—*Windthrown Engelmann spruce, Fraser Experimental Forest, Colorado.*

Above Average:

1. Valley bottoms parallel to the direction of prevailing winds.
2. Gentle middle south and west slopes not protected to the windward.
3. Moderate to steep middle, and all upper north- and east-facing slopes.
4. Moderate to steep middle south- and west-facing slopes protected by higher ground not far to windward.

Very High:

1. Ridgetops.
2. Saddles in ridges.
3. Moderate to steep middle south- and west-facing slopes not protected to the windward.
4. All upper south- and west-facing slopes.

The risk of windfall in these situations is increased at least one category by such factors as poor drainage, shallow soils, defective roots and boles, and overly dense stands. Conversely, the risk of windfall is reduced if the stand is open-grown or composed of young, vigorous, sound trees. All situations become very high risk if exposed to special topographic situations, such as gaps or saddles in ridges at high elevations to the windward that can funnel winds into the area *(1,3,13)*.

The spruce beetle *(Dendroctonus rufipennis)* is the most serious insect pest of Engelmann spruce *(86)*. It is restricted largely to mature and overmature spruce, and epidemics have occurred throughout recorded history. One of the most damaging outbreaks was in Colorado from 1939 to 1951, when beetles killed nearly 6 billion board feet of standing spruce *(64)* (fig. 7). Damaging attacks have been largely associated with extensive windthrow, where downed trees have provided an ample food supply for a rapid buildup of beetle populations. Cull material left after logging has also caused outbreaks, and there are examples of large spruce beetle populations developing in scattered trees windthrown after heavy partial cutting. The beetle progeny then emerge to attack living trees, sometimes seriously damaging the residual stand. Occasionally, serious spruce beetle outbreaks have developed in overmature stands with no recent history of cutting or windfall, but losses in uncut stands that have not been subjected to catastrophic wind storms have usually been no greater than normal mortality in old growth *(13)*.

Spruce beetles prefer downed material to standing trees, but if downed material is not available, then standing trees may be attacked. Large, overmature trees are attacked first, but if an infestation persists, beetles will attack and kill smaller trees after the large trees in the stand are killed. In the central

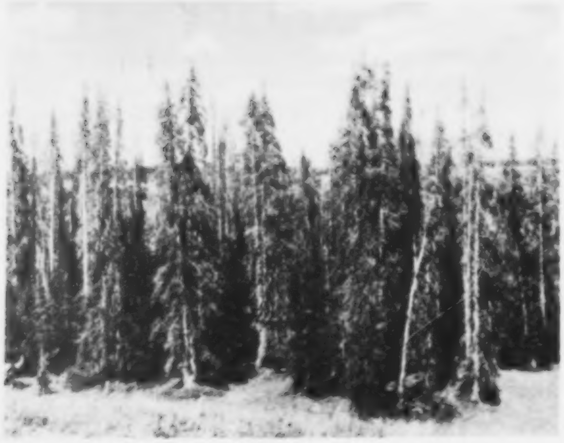

Figure 7—*Engelmann spruce killed by spruce beetles, White River Plateau, Colorado.*

Rocky Mountains susceptibility to beetle attack can vary by location; the following sites are arranged from most to least susceptible: (1) trees in creek bottoms, (2) good stands on benches and high ridges, (3) poor stands on benches and high ridges, (4) mixed stands, and (5) immature stands *(59,85)*. Analysis of past infestations suggests the following kinds of stands are susceptible to outbreaks: (1) single- or two-storied stands, (2) high proportions of spruce in the overstory, (3) basal area of 34 m/ha (150 sq ft^2/acre) or more in older and larger trees, and (4) an average 10-year periodic diameter growth of 1.0 cm (0.4 in) or less *(87)*.

The western spruce budworm *(Choristoneura occidentalis)* is another potentially dangerous insect attacking Engelmann spruce and subalpine fir *(40)*. Although spruce and fir are among the preferred hosts, budworm populations have been held in check by combinations of several natural control factors—parasites, predators, diseases, and adverse climatic conditions. The potential for future outbreaks is always present, however. An excellent summary of the ecology, past insecticidal treatments, and silvicultural practices associated with western spruce budworm in northern Rocky Mountain forests is given by Carlson *et al.* *(28)*.

The most common diseases of Engelmann spruce are caused by wood-rotting fungi that result in loss of volume and predispose trees to windthrow and windbreak *(46)*. In a recent study of cull indicators and associated decay in Colorado, the major root and butt fungi in mature to overmature Engelmann spruce were identified as *Phellinus nigrolimitatus, Flammula alnicola, Polyporus tomentosus* var. *curnatua, Gloeocystidiellum radiosum*, and *Coniophora puteana*. Trunk rots, which caused 88 percent of the decay, were associated with *Phellinus pini, Haematosterceum sanguinolentum, Echinodontium sulcatum*, and *Amylosterceum chailletii*. Spruce broom rust *(Chrysomyxa arctostaphyli)* is also common in spruce-fir forests. It causes bole deformation, loss of volume, and spiketops; increases susceptibility to windbreak; and provides infection courts for decay fungi in spruce *(20,46)*.

Dwarfmistletoe *(Arceuthobium microcarpum)* causes heavy mortality in spruce in Arizona and New Mexico, but it has a limited range in the Southwest and is not found elsewhere *(44)*.

Engelmann spruce does not prune well naturally. Thin bark and the persistence of dead lower limbs make it susceptible to destruction or severe injury by fire (fig. 8). Many root and trunk rots in old growth appear to be associated with fire injury. Because of the climate where spruce grows, the risk of fire is less than in warmer and drier climates *(20)*.

Special Uses

Engelmann spruce—subalpine fir forests occupy the greatest water yielding areas in the Rocky Mountains. They also provide timber, habitats for a wide variety of game and nongame wildlife, forage for livestock, and recreational opportunities and scenic beauty *(5)*. However, these properties are indigenous to where spruce grows rather than to any special properties associated with the species.

The lumber of spruce is likely to contain many small knots. Consequently, it yields only small amounts of select grades of lumber, but a high proportion of the common grades *(70)*. In the past, spruce was used principally for mine timbers, railroad ties, and poles. Today, much of the lumber is used in home construction where great strength is not required, and for prefabricated wood products. In recent years, rotary-cut spruce veneer has been used in plywood manufacture. Other uses of spruce include specialty items such as violins, pianos and aircraft parts *(22,63)*.

The pulping properties of Engelmann spruce are excellent. Long fibers, light color, and absence of resins permit trees to be pulped readily by the sulfite, sulfate, or groundwood processes *(22,101)*. The species has been used for pulp in the northern Rocky

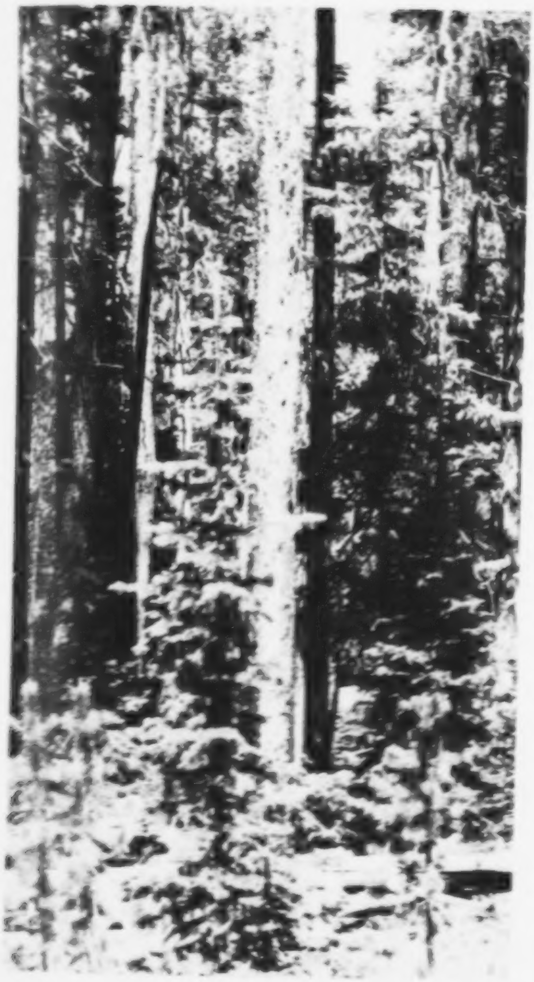

Figure 8—*Engelmann spruce does not prune well naturally. This old-growth stand still retains many dead lower branches.*

Mountains but not in the central or southern Rocky Mountains.

Genetics

Population Differences

Available information on population differences of Engelmann spruce is limited to a few studies. For example, spruce trees from high-elevation seed sources and northern latitudes break dormancy first in the spring, and, when grown in low-elevation nurseries with low- and middle-elevation seed sources, are the first to become dormant in the fall. Conversely, low-elevation and southern latitude seed sources frequently are more resistant to spring frosts, but are less winterhardy than middle- and high-elevation seed sources *(38)*. In one study that compared seedlings from 20 seed sources, ranging from British Columbia to New Mexico, planted at an elevation of 9,600 feet in Colorado, seedlings from northern latitudes and lower elevations made the best height growth *(93)*. Overall survival from all sources was 73 percent with no significant differences among sources.

Races and Hybrids

There are no recognized races or geographical varieties of Engelmann spruce. There is abundant evidence that natural introgressive hybridization between Engelmann and white spruce occurs in sympatric areas, especially around Glacier Park in Montana *(32)*. It has been suggested that Engelmann and Sitka spruces cross in British Columbia, but it seems more likely that the crosses are between Sitka and white spruce. Engelmann spruce has been artificially crossed with several other spruces, but with only limited success *(38)*.

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Picea glauca (Moench) Voss

White Spruce

Pinaceae **Pine family**

Hans Nienstaedt and John C. Zasada

White spruce *(Picea glauca)*, also known as Canadian spruce, skunk spruce, cat spruce, Black Hills spruce, western white spruce, Alberta white spruce, and Porsild spruce, is adapted to a wide range of edaphic and climatic conditions of the Northern Coniferous Forest. The wood of white spruce is light, straight grained, and resilient. It is used primarily for pulpwood and as lumber for general construction.

Habitat

Native Range

White spruce (fig. 1) has a transcontinental range, from Newfoundland and Labrador west across Canada along the northern limit of trees to Hudson Bay, Northwest Territories, and Yukon. It almost reaches the Arctic Ocean at latitude 69° N. in the District of Mackenzie in the Northwest Territories *(149)*. In Alaska, it reaches the Bering Sea at Norton Bay and the Gulf of Alaska at Cook Inlet. In British Columbia, it comes within 100 km (60 mi) of the Pacific Ocean in the Skeena Valley where it overlaps with Sitka spruce *(Picea sitchensis)*, and from there it extends south through British Columbia, and east through Alberta and Manitoba to Lake Winnipeg and south and east through northern Minnesota and Wisconsin, central Michigan, northeastern New York, and Maine. The contiguous distribution shown extending south in the Rocky Mountains into Montana actually may be outliers similar to those found further south in Montana, in the Black Hills in Wyoming and South Dakota (approximately latitude 44° N.), and at Cypress Hills in Saskatchewan *(149)*.

White spruce grows from sea level to about 1520 m (5,000 ft) elevation. It is found near 610 m (2,000 ft) on the central tableland of Labrador north of latitude 52° N. *(108)*, and in Alaska white spruce forests approach 910 m (3,000 ft) at about latitude 68° N. in the Dietrich River Valley on the south slope of the Brooks Range *(26)*. It reaches 1160 m (3,800 ft) in the timberline forest at latitude 61° N. in the Liard Range in the Northwest Territories *(79)*, and farther south in the Rocky Mountains it is the dominant species from the edge of the plains at 1220 m (4,000 ft) to about 1520 m (5,000 ft). In interior British Columbia, white spruce grows at elevations as low as 760 m (2,500 ft) in the east Kootenay Valley *(130)*.

Climate

White spruce has been described as a "plastic" species because of its ability to repopulate areas at the end of glaciation. It grows under highly variable conditions, including extreme climates and soils.

In the north, the position of the tree line has been correlated to various factors, including the 10° C (50° F) isotherm for mean July temperature, cumulative summer degree days, position of the Arctic front in July, mean net radiation (especially during the growing season), and low light intensities (see review *39*). None of the variables strictly define the northern limit of spruce, and in northern Alaska the presence of mountainous topography makes it difficult to determine controlling factors *(26)*. Other biotic and abiotic variables affecting the northern and altitudinal distribution include lack of soil, low fertility, low soil temperature, fire, insects, disease, human impact, soil stability, and others *(39,158,159)*.

The southern limit of the belt in which white spruce forms more than 60 percent of the total stand roughly follows the 18° C (64° F) July isotherm. The association is particularly close northeast of Lake Superior; in the Prairie Provinces, the species' limit swings north of the isotherm.

At the northern limit of the species' range, climatic extremes are significant. For example, –54° C (–65° F) in January and 34° C (94° F) in July were recorded extremes in one study area *(102,158)*. Mean daily temperatures of –29° C (–20° F) for January are recorded throughout the species' range in Alaska, Yukon, and Northwest Territories, while mean daily July temperatures range from about 21° C (70° F) in the extreme southeastern area of distribution to 13° C (55° F) throughout much of Alaska and Canada. Maximum temperatures as high as 43° C (110° F) have been recorded within the range in Manitoba. Mean annual precipitation ranges from 1270 mm (50 in) in Nova Scotia and Newfoundland to 250 mm (10 in) through the Northwest Territories, Yukon, and parts of Alaska. Conditions are most severe, however, along the southern edge of distribution through Alberta, Saskatchewan, and Manitoba, where a mean annual precipitation of from 380 to 510 mm (15 to 20

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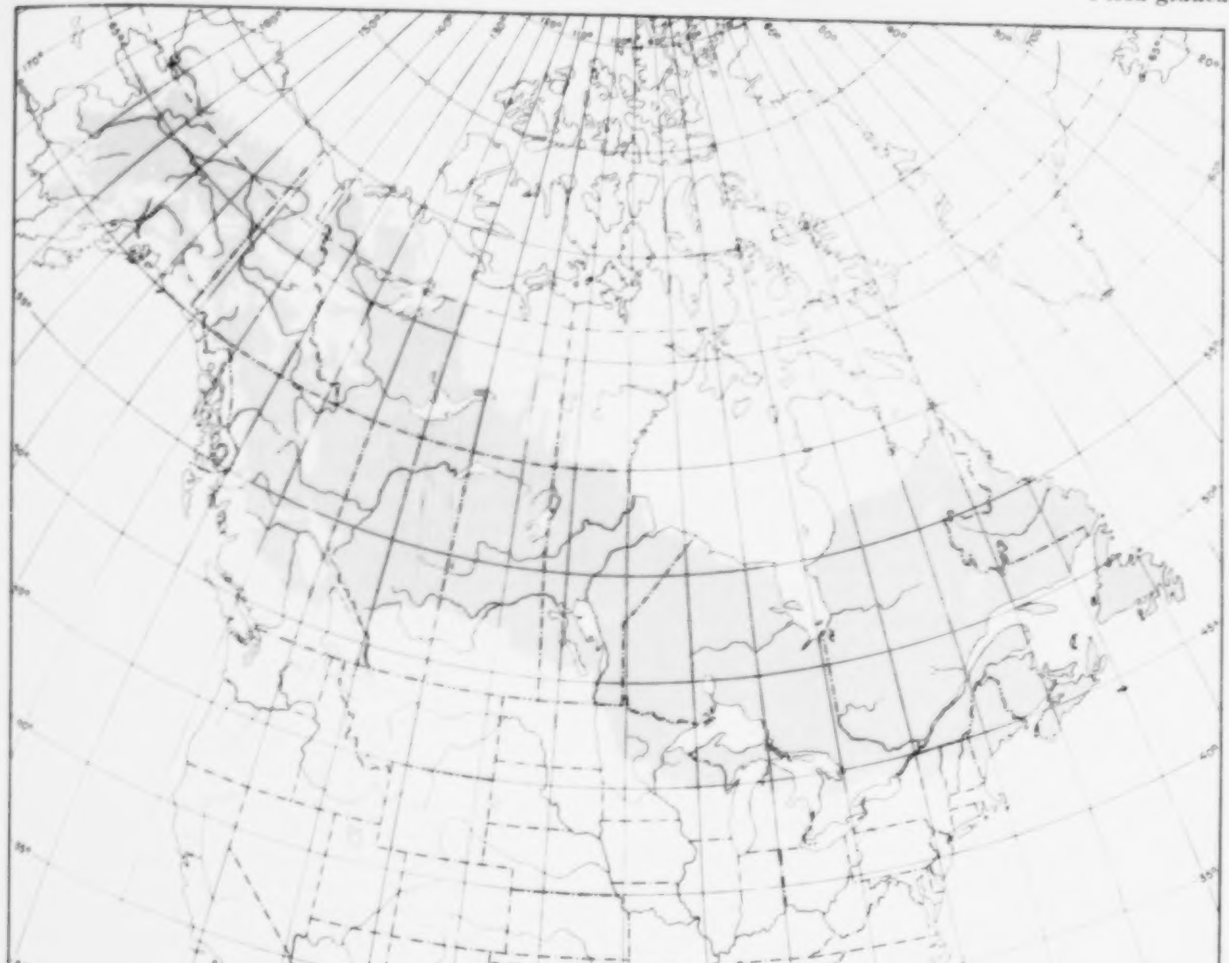
120°
115°
110°
105°
100°
95°
90°
85°
80°
75°
70°
1984

Figure 1—*The native range of white spruce.*

in) coincides with mean July daily temperature maxima of 24° C (75° F) or more.

The growing season ranges from about 180 days in parts of Maine to about 20 days in parts of Canada. Generally, however, white spruce grows in regions where the growing season exceeds 60 days *(108)*.

Photoperiod varies continuously over the range of the species from approximately 17 hours at summer solstice along the southern edge of the species' distribution to 24 hours north of the Arctic Circle in Alaska and parts of northern Canada.

Soils and Topography

White spruce grows on a wide variety of soils of glacial, lacustrine, marine, or alluvial origin. Substrata represent the geological eras from Precambrian to Cenozoic and a great variety of rock formations, including granites, gneisses, sedimentaries, slates, schists, shales, and conglomerates *(134,158)*. Some bedrocks are acidic, such as granites, and others are basic dolomites and limestones.

Mature northern white spruce stands have well-developed moss layers that significantly affect the mineral soil. The layer is most highly developed in regions with adequate moisture conditions and is dominated by feather mosses (e.g., *Hylocomium splendens, Pleurozium schreberi, Ptilium cristacastrensis,* and *Dicranum* spp.) rather than *Sphagnum* species *(92,159)*. In the far north, total depth of the live moss-organic mat frequently is from 25 to 46 cm (10 to 18 in) or more. Development is, in part, regulated by flooding and stand composition. Stands in which hardwoods are mixed with white spruce tend to have shallower, discontinuous moss layers. The layer is a strong competitor for nutrients and an effective insulator that reduces temperature in the rooting zone. The temperature reduction varies with latitude and climatic regime. In Alaska, Yukon, and the Northwest Territories, soil temperatures can reach the point at which permafrost is developed and maintained *(53,158,161)*.

Podzolic soils predominate over the range of the species, but white spruce also grows on brunisolic, luvisolic, gleysolic, and regosolic soils. On sandy podzols, it is usually a minor species, although white spruce is common on sand flats and other coarse-textured soils in the Georgian Bay area. It grows on shallow mesic organic soils in Saskatchewan, and in central Yukon on organic soils with black spruce *(85,134,149)*.

White spruce is able to grow on extremely diverse sites, but to achieve the best development it is generally more demanding than associated conifers. The range of sites supporting the species becomes more limited northward with increasing climate severity *(149)*.

In the Algoma District of Ontario, the species is a major component of the stands on calcareous podzol loams and clays and shows exceptionally good development on melanized loams and clays. In Saskatchewan, it does best on moderately well-drained clay loams *(84)*; in Alberta Mixedwoods, the best development is on well-drained lacustrine soils *(60)*. Further north in Canada and Alaska, particularly productive stands are found on moist alluvial soils along rivers *(78,79,90,162)* and on south-facing upland sites *(41,158)*.

White spruce grows on both acid and alkaline soils and acidity (pH) values from 4.7 to 7.0 and perhaps higher are probably optimum *(10,141,149,176)*. On the floodplains of the northern rivers, pH may vary from 5.0 to 8.2 *(194)*. In the Northwest Territories, the species grows in the alpine fir forest on strongly acid soils with a surface pH of from 4.0 to 4.5, increasing with depth to pH 5.5 at 15 cm (6 in); but at somewhat lower elevations, the mixed coniferous forest soils have a pH of 4.0 at the surface with pH 8.0 at 38 cm (15 in) depth. Good growth of white spruce on alkaline soils has also been reported in Mixedwoods in the Prairie Provinces *(141)*. In New York, one factor common to most white spruce locations is an abundant calcium supply. Of the wide range of sites and soils on which white spruce grows, soils in the orders Alfisols and Inceptisols are most common.

The species also tolerates a range of fertility levels. On the alluvial soils along northern rivers, nitrogen may vary from 0.2 to 0.01 percent and phosphorus from 10 to 2 p/m. On adjacent upland soils derived from loess parent material, nitrogen may vary from 0.1 to 0.4 percent and phosphorus from 10 to 3 p/m *(194)*.

Good growth requires a dependable supply of well-aerated water, yet the species will tolerate a wide range of moisture conditions. It will not tolerate stagnant water that reduces the rooting volume. On the other hand, white spruce will grow on dry sites if they are fertile.

Soil fertility, soil moisture, and physical properties are interrelated. Moisture alone will not improve yields unless it is associated with increased fertility *(149)*. Nor will increased moisture be beneficial if soil structure is less than optimum. In Riding Mountain, Manitoba, for example, lower yields on the moist sites have been attributed to the higher clay content and massive structure when wet and columnar structure in dry conditions *(73)*.

Table 1—Minimum soil fertility standards for planting Wisconsin native conifers *(146)*[1]

Item	Jack pine	Red pine	White pine	White spruce
Approx. site index,[2] m	16	17	18	16
ft	53	57	60	52
Approx. optimum range of pH[3]	5.0 to 7.0	5.2 to 6.5	4.7 to 7.3	4.7 to 6.5
Silt and clay, pct	7.0	9.0	15.0	35.0
Organic matter, pct	1.0	1.3	2.5	3.5
Exchange capacity, meq/100g	2.5	3.5	5.7	12.0
Total N, pct	0.04	0.05	0.10	0.12
Available P, kg/ha	13.4	28.0	33.6	44.8
lb/acre	12	25	30	40
Available K, kg/ha	56.0	78.5	112.1	145.7
lb/acre	50	70	100	130
Exchangeable Ca, meq/100g	0.50	0.80	1.50	3.00
Exchangeable Mg, meq/100g	0.15	0.20	0.50	0.70

[1] Minimum is an amount sufficient to produce 126 to 157 m^3/ha (20 to 25 cords/acre) at 40 years. All nutrients are given in terms of elements, not oxides.

[2] Base age 50 years.

[3] Data for values above pH 6.5 are insufficient; the range is strongly influenced by climatic conditions.

Other soil factors that must be carefully considered include the depth to ground water, permeability (especially of surface layers), presence of hardpans or claypans, and the mineralogical composition of the parent material.

Minimum soil-fertility standards for white spruce are higher than for other conifers commonly planted in the Lake States *(176)* (table 1).

Fertility requirements for white spruce based on foliar analyses are in percent of dry matter: nitrogen 1.50 to 2.50; phosphorus 0.18 to 0.32; potassium 0.45 to 0.80; magnesium 0.10 to 0.20; and calcium 0.15 to 0.40. At the lower end of the range, plants will respond to fertilizer. These data are from sand-culture experiments and are definitely provisional *(152)*; however, except for calcium, they are in line with values published for 3-year-old seedlings in the nursery *(71)*.

Little specific information is available on the effects of fertilizer in natural stands or plantations of white spruce, but growth gains have been reported after treatments to overcome nutrient deficiencies *(141)*. Response of established older stands and new plantations to fertilization can occur within a year of treatment *(9,156)*. Observations in progeny test plots in northern Wisconsin suggest that a hand application of 10-10-10 fertilizer may shorten the period of planting shock. In a nursery in which prolonged use may have depleted exchangeable bases and probably micronutrients, an application of micronutrient and major nutrient fertilizers resulted in a greatly increased volume of root systems and their absorbing capacity, and in a decreased top-root ratio. But indiscriminate use of micronutrient fertilizers together with nitrogen fertilizers may reduce seedling quality, making plants succulent, with a high top-root ratio *(71)*.

White spruce stand development can significantly affect forest floor composition and biomass and mineral soil physical and chemical properties. The magnitude of these effects will vary with site conditions and disturbance history of the site. On sites in Alaska, organic layers accumulate to greater depths in mature spruce stands than in hardwood stands growing on similar sites. As a result, soil temperatures decrease and, in extreme cases, permafrost develops *(161,163)*. Acidity of the mineral soil in spruce plantations established on abandoned farmland in Ontario decreased by 1.2 pH units over a 46-year period *(10)*. Soil conditions under 40-year-old white spruce differed significantly in some respects from that under aspen, red pine, and jack pine growing on the same soil type; relative differences among species varied with specific nutrients *(2)*.

Associated Forest Cover

Eastern Forest—The forest cover type White Spruce (Society of American Foresters Type 107) *(40)* is found in either pure stands or mixed stands in which white spruce is the major component. Associated species include black spruce, paper birch *(Betula papyrifera)*, quaking aspen *(Populus tremuloides)*, red spruce *(Picea rubens)*, and balsam fir *(Abies balsamea)*. Yellow birch *(B. alleghaniensis)* and sugar maple *(Acer saccharum)* are sometimes included in the community mix.

The type is minor and confined to abandoned fields in New England and the Maritime Provinces, and within the fog belt farther north in Quebec and Labrador. It is more widespread elsewhere in eastern Canada and as far north as the tree line in Ungava and along Hudson Bay.

In northern Quebec, the lichen *(Cladonia)* woodland, the feathermoss forest, and the shrub forest with bog birch *(B. nana)* and heath species are common white spruce communities.

White spruce is an associated species in the following Eastern Forest cover types:

Boreal Forest Region

1	Jack Pine
5	Balsam Fir
12	Black Spruce
16	Aspen

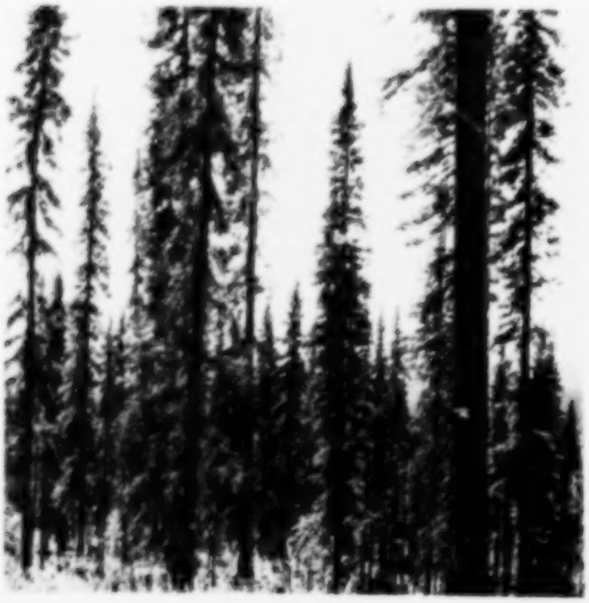

Figure 2—*White spruce stand on the Yukon-Tanana Upland in interior Alaska, regenerated by the shelterwood system.*

18	Paper Birch
38	Tamarack

Northern Forest Region

15	Red Pine
21	Eastern White Pine
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
27	Sugar Maple
30	Red Spruce–Yellow Birch
32	Red Spruce
33	Red Spruce–Balsam Fir
37	Northern White-Cedar
39	Black Ash–American Elm–Red Maple

In three of these types, Aspen (Type 16), Paper Birch (Type 18), and Red Pine (Type 15), white spruce attains increasing importance in the stand composition as the succession progresses and more tolerant species take over.

Western Forest—White Spruce (Type 201) is the pure white spruce forest in the West. In Alaska and the Northwest Territories, the type is largely confined to stream bottoms, river floodplains and terraces, and warm, south-facing upland sites (fig. 2). Farther south in British Columbia and Alberta, it has broader distribution from as low as 760 m (2,500 ft) to 1520 m (5,000 ft).

Associated tree species in Alaska include paper birch, quaking aspen, black spruce, and balsam poplar (*Populus balsamifera*). In Western Canada, subalpine fir (*Abies lasiocarpa*), balsam fir, Douglas-fir (*Pseudotsuga menziesii*), jack pine (*Pinus banksiana*), and lodgepole pine (*P. contorta*) are important associates.

The type varies little and generally comprises closed stands. White spruce plant communities in interior Alaska include white spruce/feathermoss; white spruce/dwarf birch/feathermoss; white spruce/avens (*Dryas*)/moss; and white spruce/alder (*Alnus* spp.)/blue-joint (*Calamagrostis canadensis*) (*32, 43, 61*). Two communities are common in northwestern Canada and in Alaska: (1) white spruce/willow (*Salix* spp.)/buffaloberry (*Shepherdia* spp.)/northern goldenrod (*Solidago multiradiata*)/ crowberry (*Empetrum* spp.) and (2) white spruce/willow/buffaloberry/huckleberry (*Gaylussacia* spp.)/dewberry (*Rubus* spp.)/peavine (*Lathyrus* spp.).

In White Spruce–Aspen (Type 251), either species may be dominant, but each species must make up at least 20 percent of the total basal area. Paper birch and black spruce may also be represented in Alaskan stands along with balsam fir and lodgepole pine in Canadian stands. The type is common throughout western Canada at lower elevations and in all of interior Alaska. Associated shrubs in Alaska are American green alder (*Alnus crispa*), willows, common bearberry (*Arctostaphylos uva-ursi*), soapberry, highbush cranberry (*Viburnum edule*), and mountain cranberry (*Vaccinium vitis-idaea*). Associated shrubs in the Prairie Provinces are common snowberry (*Symphoricarpos albus*), red-osier dogwood (*Cornus stolonifera*), western serviceberry (*Amelanchier alnifolia*), and western chokecherry (*Prunus virginiana* var. *demissa*).

White Spruce–Paper Birch (Type 202) is defined similarly to White Spruce–Aspen in that either spruce or birch may be dominant as long as each species makes up at least 20 percent of the basal area. Aspen, lodgepole pine, subalpine fir, and black spruce are associated species. The type is common in Western Canada and in Alaska from the Arctic Circle to the Kenai Peninsula. Undergrowth species include willow, American green alder, highbush cranberry, prickly rose (*Rosa acicularis*), mountain cranberry, bunchberry (*Cornus canadensis*), and Labrador-tea (*Ledum groenlandicum*).

Whereas White Spruce–Aspen and White Spruce–Paper Birch are successional stages leading to the pure White Spruce type, Black Spruce–White Spruce (Type 253) may be a climax near the altitudinal and northern treeline. But black spruce may be replacing white spruce on some intermediate sites on older river terraces *(160)*. Black Spruce–White Spruce is the lichen-woodland type from Hudson Bay to northwestern Alaska along the treeline as well as in open stands at alpine treeline sites in interior Alaska and northwestern Canada. It is also found on sites intermediate to the two species, such as older terraces above the floodplain. Paper birch, tamarack *(Larix laricina)*, balsam poplar, aspen, and balsam fir may be found within the stands. In open stands near the treeline, resin birch *(Betula glandulosa)*, alder, and willows may form a continuous shrub cover that on drier sites may be replaced by mats of feathermosses and *Cladonia* lichens. Labrador-tea, bog blueberry *(Vaccinium uliginosum)*, mountain cranberry, and black crowberry *(Empetrum nigrum)* are other common shrubs within the type.

In addition to these three tree cover types in which white spruce is a major component, the species is an associate in the following Western Forest cover types:

203	Balsam Poplar
204	Black Spruce
206	Engelmann Spruce–Subalpine Fir
217	Aspen
218	Lodgepole Pine
237	Interior Ponderosa Pine
252	Paper Birch
254	Black Spruce–Paper Birch

Several of these types are intermediate in the succession. Paper Birch may advance through White Spruce–Paper Birch to pure White Spruce. Balsam Poplar (Type 203) is eventually overtopped and replaced by white spruce; on some sites the process is very slow. Aspen often precedes the more tolerant spruce and fir forests, and lodgepole pine may be replaced by white spruce in northern latitudes.

In the Canadian boreal spruce-fir forest, American green alder is the most widespread tall shrub, with littletree willow *(Salix arbusculoides)*, gray willow *(S. glauca)*, and Bebb willow *(S. bebbiana)* important in the western range. Mountain maple *(Acer spicatum)*, showy mountain-ash *(Sorbus decora)*, and American mountain-ash *(S. americana)* are important in the East. Highbush cranberry, red currant *(Ribes triste)*, prickly rose, and raspberry *(Rubus idaeus)* are the most common medium to low shrubs. The most wide-ranging members of the herb-dwarf shrub stratum are fireweed *(Epilobium angustifolium)*, one-sided wintergreen *(Pyrola secunda)*, one-flowered wintergreen *(Moneses uniflora)*, northern twinflower *(Linnaea borealis)*, naked bishops-cap *(Mitella nuda)*, bunchberry, dwarf rattlesnake-plantain *(Goodyera repens)*, stiff clubmoss *(Lycopodium annotinum)*, and horsetail *(Equisetum* spp.) *(91)*.

An average of 24 bryophytes (17 mosses and 7 liverworts) occur in Canadian white spruce-fir stands *(92)*. The most common mosses are *Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis, Dicranum fuscescens,* and *Drepanocladus uncinatus*. The most common liverworts are *Ptilidium pulcherrimum, P. ciliare, Lophozia* spp., and *Blepharostoma trichophyllum*. Some common lichens are *Peltigera apthosa, P. canina, Cladonia rangiferina, C. sylvatica, C. alpestris, C. gracilis,* and *Cetraria islandica*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—White spruce is monoecious. Reproductive buds are differentiated at the time shoot growth ceases, the year before flowering and seed dispersal *(35,118)*. The process lasts about a week. In British Columbia, it occurs during the last 2 weeks of July over a wide range of sites; this suggests that it may occur at about the same time throughout much of the species' range. Development of reproductive buds continues for 2 to 2.5 months and coincides with shoot maturation. The male buds become dormant first (about October 1 at Prince George, BC) followed by the vegetative and female buds about 2 weeks later *(118)*.

Cone-crop potential can be predicted in several ways. An early indication of a potential crop can be abnormally hot, dry weather at the time of bud differentiation, particularly if the current and preceding cone crops have been poor. Estimates of cone crop potential can be made by counting female reproductive buds in fall or winter. Differentiating male and female buds from vegetative buds is difficult, but the external morphology of the buds, and their distribution within the crown, enables the practiced observer to make the distinction *(35)*. Female buds are concentrated in the top whorls. On 17-year-old grafts, the most productive was the 4th whorl from the top, and the productive zone averaged 6.4 whorls *(112)*. In light crop years, the highest cone concentration is closer to the top than in intermediate or heavy crop years. Male buds generally are located in the middle to lower crown *(38)*.

In the spring, renewed cell division and growth begin before the first evidence of bud elongation. In British Columbia, this is 6 weeks before pollination at low elevations and 8 weeks before pollination at high elevations *(119)*. Meiosis takes place during this period about 3 weeks before maximum pollen shedding. Female receptivity coincides with pollen shedding and usually lasts from 3 to 5 days in May, June, or July depending on geographic location and climate. The southern areas definitely have earlier dispersal than northern areas; however, peak dispersal at latitude 48–50° and 65° N. can occur on the same calendar date *(106,108,149,193)*. Pollination is delayed up to 5 weeks at higher elevations *(119,193)*. The latest pollen dispersal occurs near elevational and latitudinal treeline.

The time of pollen shedding and female receptivity is undoubtedly temperature dependent and may vary as much as 4 weeks from year to year *(44)*. Pollen dispersal shows a marked diurnal pattern dependent on temperature, humidity, and wind *(193)*.

The period of peak pollination and female receptivity is a critical stage in seed production and is easily disrupted by adverse weather such as rain and frost *(102,106,181)*. Such events can seriously reduce a promising seed crop.

Before pollen dispersal, male flowers are red and succulent; water can be squeezed from the conelet in a substantial drop. Moisture content (percentage of dry weight) was 500 to 600 percent greater than dry weight before pollen dispersal began and dropped precipitously as the male flower dried and pollen was dispersed. Just before shedding, the males are approximately 10 to 12 mm (0.4 to 0.5 in) long. Then the color changes from red to yellow and the conelet is almost dry when squeezed. This is the ideal time for collecting pollen. After the pollen is shed, the structure turns brown and soon falls.

At maximum receptivity, females are erect, 20 to 25 mm (0.8 to 1.0 in) long, and vary in color from green to deep red. Within an individual tree, the color is uniform. When receptive, the scales are widely separated, but they close shortly after pollination and the cones begin to turn down and gradually dull in color. Turning down takes from 2 to 4 weeks and occurs when the cone is growing most rapidly.

Fertilization occurs from 3 to 4 weeks after pollination *(103,119,128)*. Full size and maximum cone water content and fresh weight are attained in late June or early July. The final cone size may vary considerably from year to year *(193)*; it is determined by the weather the previous season, weather during cone expansion, and heredity.

The primary period of embryo growth occurs after cones attain maximum size. Cotyledons appear in middle to late July and embryo development is completed in early to late August *(103,119,128,188)*. Seed development can vary as much as 3 weeks from year to year *(33)*, and cotyledon initiation may differ from 1 to 3 weeks between high and low sites. Embryos have matured on the same date at both high and low elevations *(119)*; however, there can be large differences among elevations in time of seed maturation *(188)*.

The maturation process evidently continues after embryos attain physical and anatomical maturity *(33,177,183)*. Cone dry weight generally increases during this period. Weather is critical to the production of high quality seed. In high elevation and high latitude populations, immature seed with poorly developed embryos are produced during cold growing seasons *(183,193)*. In general, seed quality is highest in years of heavy seed production and lowest in years of low seed production. Cones ripen in August or September from 2 to 3 months after pollen shedding *(21,167,177,183)*.

Cone opening coincides with moisture contents of from 45 to 70 percent and specific gravities of from 0.6 to 0.8 *(21,177,193)*. Cone firmness, seed coat color, seed brittleness, and various flotation tests are indicators of cone and seed maturity *(141)*. Cone color can also be used; but because female cone color can be red, pink, or green *(153)*, no standardized cone color changes are associated with maturity. Most authorities agree on the importance of observing cones closely during the last stages of maturity so that the optimum collection period is not missed.

White spruce seeds can be collected from 2 to 4 weeks before they ripen and seed quality improved by storing under cool (4° to 10° C (40° to 50° F)), ventilated conditions. Collection date and method of cone handling affect prechilling required for germination and early seedling growth. No specifics have been recommended for the best cone handling procedures *(33,177,183)*.

Seed Production and Dissemination—Cones and seeds have been produced by 4-year-old trees *(149)*. Production "in quantity" on 10- to 15-year-old trees has been reported, but it is usually low in younger trees and depends on site and season. Seed production in quantity begins at age 30 or older for most natural stands *(44,117)*. The interval between good to excellent cone and seed crops varies with site and geographic location. On good sites, good to excellent years can occur at 2- to 6-year intervals but may be as many as 10 to 12 years apart *(88,167,184,192)*. Excellent seed years may be related to hot, dry summers at the time of bud differentiation *(112)*. They are always followed by poor ones; the alternation can result from carbohydrate and nutrient deficiencies or the lack of sites in the crown able to produce reproductive buds *(117)*.

A mixture of gibberellins, GA4/7, has been found to substantially increase female flowering in white spruce *(15,121)*. Treatment of elongating shoots was effective, but application to dormant shoots was not

(16). Fertilization with ammonium nitrate has also been successful in promoting flowering *(68)*.

Both the initiation and pattern of seed dispersal depend on the weather. Cool, wet, or snowy weather delays the onset of dispersal and causes cones to close after dispersal has begun. Cones reopen during dry weather. A small number of seeds are usually dispersed in August, but most of the seeds fall in September *(30,167,186,192,193)*. Early- and late-falling seeds have a lower viability than seeds falling during the peak period *(167)*. Cones can remain on the tree from 1 to 2 years after the majority of seeds are dispersed. Cone opening and seed dispersal pattern can vary among trees in the same stand *(186)*.

Average weight per seed varies from 1.1 to 3.2 mg (0.02 to 0.05 grains) *(64,193)*, and there are approximately 500,000 seeds per kilogram (226,000/lb) *(155)*. From 8,000 to 12,000 cones may be produced by individual trees in good years. This corresponds to approximately 35 liters (1 bushel) or about 250,000 seeds *(64)*. Yields in the far north are less *(184)*. Cone production in mature spruce stands occurs primarily in dominant and codominant trees with sporadic and low production in intermediate and suppressed trees *(167)*.

The total number of seeds per cone varies significantly among trees and regions—from 32 to 130 have been reported *(87,167,192)*. Seeds produced on the apical and basal scales are not viable; therefore, the number of viable seeds per cone is much lower—from 12 to 34 and from 22 to 61 full seeds per cone for open and control pollinations, respectively *(87)*.

Seed dispersal as measured by seed trapping varies with seed year and from day to day. In Manitoba, the maximum annual total seedfall was 1400/m^2 (130/ft^2), and 59 percent were filled. The seed rain exceeded 290/m^2 (26.9/ft^2) in 5 of the 10 years, and 40 to 71 percent of these were filled; for 3 years it was less than 10/m^2 (0.9/ft^2), and of these 2 to 36 percent were filled *(167)*. In Alaska, maximum total seed rain in one stand over a 13-year period was 4,000 seeds/m^2 (371.7/ft^2). Seed rain exceeded 1,000 seeds/m^2 (92.9/ft^2) in 3 years and was between 400 and 500 seeds/m^2 (37.1 and 46.4/ft^2) in 2 other years. In the remaining years, seed rain was less than 100/m^2 (9.3/ft^2) *(184)*.

White spruce is primarily wind-dispersed, and the time in flight and distance of flight for individual seeds was variable and depended on conditions at the time of dispersal *(191)*. The quantity of seed reaching a given area drops precipitously with distance from the seed source. At 50, 100, 200, and 300 m (162.5, 325.0, 650.0, 975.0 ft), seed rain may be as low as 7, 4, 0.1, and 0.1 percent of that in the stand. The actual percentage of seeds reaching various distances may vary among sites within a local area and among geographical areas *(30,186)*.

White spruce seed collection is expensive, but cost can be reduced by robbing the cone-caches of red squirrels. The viability of seed from cached cones does not vary between the time squirrels begin to cache cones in quantity and the time the last cones are cached *(164)*. Viability drops to near zero, however, after 1 to 2 years of storage in a cone cache.

White spruce rapidly regenerates the crown after topping, thereby restoring the seed-bearing capacity. In fact, topping may temporarily increase cone production *(112)*. Therefore, it is possible to reduce seed collection costs more than three times by collecting from downed tops *(138)*.

Seedling Development—White spruce seed shows conditional dormancy that varies in response to temperature and light conditions and therefore can be modified by stratification or prechilling. Optimum germination temperatures are from 10° to 24° C (50° to 75° F); maximum germination temperature is between 29° and 35° C (84° and 95° F). Minimum constant temperature is 5° C (41° F), but most germination ceases below 10° C (50° F). A diurnal fluctuation in temperature may be favorable *(27,47)*.

Prechilling or stratification at 2° to 4° C (36° to 39° F) is recommended for testing seed lots and for improving germination capacity, energy, and survival in the nursery of spring-sown seed. Stratification is not always a prerequisite for complete germination, however *(27,47,171,172,193)*. Germination is epigeal *(155)*.

The period of germination under field conditions is mid-May through early August. With adequate water, seeds germinate as soon as soil surface temperatures are warm enough. Generally, germination (natural seedfall or artificial seeding in fall) is 75 to 100 percent complete by early July. Some white spruce seeds are able to withstand several wetting and drying cycles without losing their viability *(63,70,168,189)*. Germination of spring-sown seeds begins somewhat later than in fall-sown seeds but is complete in 3 to 4 weeks *(24,34)*. Adverse conditions offset germination and may delay it to the following year. Germinants developing after the middle of July have a lower survival probability than those originating in early summer *(18,49,62,67,193)*.

White spruce is capable of reproducing under mature stands of spruce and early succession tree species; however, the response is highly variable and density and percent stocking are low *(89,170)*. In Saskatchewan, for example, advanced regeneration was not present in 88 percent of the stands studied, and one-half of the remaining stands had less than

1,240 seedlings per hectare (500/acre) *(84)*. On upland sites in interior Alaska, advanced regeneration ranged from 1 to 25 percent stocking and density from 120 to 640 stems per hectare (50 to 260/acre) *(70)*.

Regeneration under established stands, whether spruce or other species, occurs on a variety of seedbeds and commonly on rotted logs *(25,164,168)*. Feathermosses (e.g., *Hylocomium* spp., *Pleurozium* spp.) and associated organic layers are the most common seedbed surfaces in mature stands *(92)*. Where the L- and F-layers are greater than from 5 to 8 cm (2 to 3 in), they greatly restrict regeneration. This is particularly true in drier western regions. Although this limitation is most often attributed to low water retention, it may be chemical inhibition (allelopathy) caused by some forest floor components, particularly lichens *(42)*. In mature stands, exposed mineral soil after windthrow and floods are the best seedbeds *(29,70,165)*. They can have stocking levels approaching 100 percent.

The average number of seeds required to produce a seedling on recently exposed mineral soil ranges from 5 to 30 *(30,36,50,69,193)*. The seed requirement increases with each year after exposure of the soil because of increasing plant competition and litter accumulation *(95)*. Receptivity of organic seedbeds is generally believed to be extremely low; seed-per-seedling ratios of 500 to 1,000 seeds or more are commonly reported in harvested areas *(36,70)*. These surfaces vary considerably, however, and their receptivity for germination and seedling establishment depend on the amount of solar radiation at the surface, type of organic substrate, degree of disturbance to the organic layers, weather conditions at the time of germination, amount of seed rain, and other biotic and abiotic factors. In undisturbed stands, seedlings are frequently found on organic matter, particularly rotted wood *(32,170,187)*. Germination and seedling establishment, although not as efficient as on mineral soil in terms of seed-to-seedling ratios, are common on organic substrates after harvest in both clearcuts and shelterwoods *(124,178)*.

A key for identifying the seedlings of North American spruce species is available *(95)*.

Optimum conditions for seedling growth have been delineated for container production of planting stock in greenhouses. The most suitable temperature conditions are alternating day/night levels as opposed to a constant temperature regime. At 400 lumens/m^2 (37.2 lumens/ft^2, or footcandles) light intensity, a 25°/20° C (77°/68° F) day/night regime is recommended for white spruce *(13,122,154)*. Temperature and light intensity effects interact: at low intensities, about 40 lumens/m^2 (3.7 lumens/ft^2), a 28°/13° C (82°/55° F) day/night regime is favorable *(11)*. A short photoperiod (14 hours or less) causes growth cessation, while a photoperiod extended with low light intensities to 16 hours or more brings about continuous (free) growth. Little is gained by using more than 16 hours low light intensity supplement once the seedlings are in the free growth mode. Long photoperiods using high light intensities of from 10,000 to 20,000 lumens/m^2 (930 to 1,860 lumens/ft^2) increase dry matter production. Increasing the light period from 15 to 24 hours may double the dry matter growth *(13,122)*.

Seedling growth can be closely controlled by manipulating the environment. Short photoperiods induce dormancy and permit the formation of needle primordia. Primordia formation requires from 8 to 10 weeks and must be followed by 6 weeks of chilling at 2° C (36° F) *(100,109,123)*. Prompt bud breaking occurs if the seedlings then are exposed to 16-hour photoperiods at the 25°/20° C (77°/68° F) temperature regime. Freedom from environmental stress (for example, lack of moisture) is essential for maintaining free growth *(99,100)*. It must be kept in mind that free growth is a juvenile characteristic. According to Logan *(99)*, it is lost when seedlings are 5 to 10 years old, but our observations suggest that it would be extremely rare in seedlings older than 5 years.

At the end of the first growing season, natural regeneration may be from 10 to 20 mm (0.4 to 0.8 in) tall. Root length is from 20 to 100 mm (0.8 to 4.0 in), depending on site and seedbed type. The stem is unbranched; the taproot normally develops lateral roots that may be from 30 to 50 mm (1 to 2 in) long *(34,62,72,89,193)*.

Natural regeneration usually does not exceed from 30 to 50 cm (12 to 20 in) in average height after 4 to 6 years. The number of branches increases significantly during this period. Lateral root length may be as much as 100 cm (39 in), but rooting depth may not increase significantly. Shoot dry weight (including foliage) increases from 0.2 to 5 g (3.09 to 77.16 grains) and root dry weight from 0.06 to 1 g (0.92 to 15.43 grains) between ages 2 and 6 *(37,70,72,89,165,168,190)*. The length of time required to reach breast height under open conditions ranges from 10 to 20 years depending on site; under stand conditions, growth to this height may take 40 or more years *(61)*.

Growth is greatest at full light intensity *(9,98)*. Reducing light intensity to 50 percent of full light reduced height growth by 25 percent, shoot weight by 50 percent, and rooting depth by 40 percent in 10-year-old seedlings; at 15 percent of full light, no spruce survived *(37)*. Control of competing herbaceous vegetation has resulted in 38 and 92 percent increases in growth 3 years after planting *(150)*.

White spruce is sensitive to transplanting shock. Check—the prolonged period of minimal growth—is considered by some forest managers to be a problem serious enough to disqualify white spruce as a plantation species. The cause of check, though not fully understood, is thought to be nutrient stress resulting from the root's inability to develop in the planting zone. Check is difficult to predict and prevent *(141,147)*, but seedling quality is a factor, and any treatment that will improve early root growth is undoubtedly beneficial *(7,9)*.

Vegetative Reproduction—Vegetative reproduction from layering is common at some latitudinal treeline sites in Canada and Alaska *(26,39)*. Layering probably is an important means of maintaining the stand when sexual reproduction is limited or nonexistent because of climatic limitations.

In the far north, the density of trees originating from layering may reach 1830/ha (740/acre) and generally is inversely related to site quality. Layering is most common in stands in which trees are open grown and the lower branches touch the ground. The branch roots when it is covered by moss, litter, or soil and organic material. The time required for an individual to become independent of the ortet (parent) is not known, but 30- to 50-year-old ramets are no longer connected with the ortet *(26)*.

Air layering on a 6-year-old tree has been successful; early May is the best time for preparing the air layers. Juvenile white spruce can be readily propagated by rooted cuttings *(54,55)*. Rooting ability varies greatly from tree to tree, but it is too low for practical use by the time most trees are 10 to 15 years old. Older trees can be grafted. Results are best in the winter (February, March) in the greenhouse, with forced rootstock in pots and dormant scions, but fall grafting is possible. Late winter–early spring grafting in the field also is possible but should be done before bud swelling becomes pronounced *(107)*.

Sapling and Pole Stages to Maturity

Growth and Yield—In white spruce, strong apical dominance of the terminal shoot leads to the excurrent growth form. Crown form may deviate substantially from the idealized conical shape because of variation in the growth of lateral branches as a result of tree and branch age, damage, or growing conditions. The most significant deviations occur near the treeline where marginal growing conditions can result in shrub-like trees. During the juvenile phase, trees can be kept growing continuously if all growth factors are within the optimum range. This is called "free growth." In older trees shoot growth is determinate; that is, the annual complement of needles is preformed in the overwintering bud.

The formation of the following year's buds in British Columbia (lat. 54° to 55° N.) begins in late April or early May with the initiation of the first bud scales. Needles for the next growing season are initiated in August and September after the period of shoot elongation. On productive forest sites, visible signs of shoot growth (flushing) are first observed in early May or early June *(108)*, 6 to 7.5 weeks after the first cell divisions signal the end of dormancy. Up to 6 weeks delay in flushing may result from a 500-m (1,640-ft) increase in elevation *(120)*. Growth of the leader and upper branches occurs over a slightly longer period than growth of lower branches *(46)*.

The time of flushing is primarily temperature dependent and therefore varies with the weather. The number of degree days accumulated at the time of flushing may vary from year to year, however, indicating that more than air temperature controls the initiation of the annual shoot-growth cycle *(8)*. Within a stand, there can also be as much as a 3-week difference among individual trees *(111,116)*. The period of shoot elongation is short. In northern Wisconsin, the period from flushing until the terminal leader had completed 95 percent of total elongation ranged from 26 to 41 days among individual trees. This is much shorter than the 6- to 11-week period reported by others *(108,149)* but agrees closely with data from central British Columbia *(120)*. In interior Alaska (lat. 64° N.), 85 to 90 percent of terminal shoot growth was completed by June 14 and 100 percent by June 28 *(70)*. The cessation of shoot growth is more dependent on photoperiod than on temperature *(120)*.

Cambial activity in Alaska (lat. 64° N.) and Massachusetts (lat. 42° N.) has been compared. The period of cambial activity is about half as long and the rate of cell division twice as great in Alaska as in Massachusetts *(56)*. Wood production (mitotic activity) was observed to begin after 11 degree days (6° C (43° F) threshold) in Alaska (early May) and Massachusetts (late April). Eighty percent of the tracheids were produced in 45 and 95 days in Alaska and Massachusetts, respectively. Variation of the same magnitude depending on site and year has been reported within a small region in Ontario *(46)*.

Culture affects growth; thinned, fertilized stands begin growing about 2 weeks earlier (late May versus early June) and have greater growth during the grand period. Termination of growth is not influenced by thinning *(157)*.

Individual white spruce trees more than 30 m (100 ft) tall and from 60 to 90 cm (24 to 36 in) d.b.h. are found on good sites throughout the range. The tallest trees reported are more than 55 m (180 ft) and from 90 to 120 cm (36 to 48 in) d.b.h. *(106,149)*.

Maximum individual tree age appears to occur on stress sites at latitudinal or elevational treeline rather than on good sites where trees attain maximum size. A partially rotted 16.5 cm (6.5 in) tree growing on the Mackenzie River Delta (above lat. 67° N.) had a 589-year ring sequence, and trees nearly 1,000 years old occur above the Arctic Circle *(51)*. On good sites, trees 100 to 250 years old are common, and the oldest trees (250 to 300 years) are frequently found in areas protected from fire, such as islands, and in relatively wet upland situations *(83,185)*.

Normal yield tables and harmonized site-index (base 100 years) curves provide estimates of growth and productivity for unmanaged stands in Alaska and western Canada. In Alaska, Farr *(41)* reported site indices at age 100 years from 15.2 m (50 ft) to 32.3 m (106 ft). Growth, yield, and selected stand characteristics for well-stocked white spruce stands in Alaska are summarized in table 2.

The lowest recorded mean annual increment (0.5 m^3/ha or 7 ft^3/acre) comes from the Mackenzie River Delta—the northernmost area of white spruce in North America.

Site indices ranging from 15.2 to 27.4 m (50 to 90 ft) (base 70-year stump age) have been reported for the Mixedwood region of Alberta *(82)*, and in the Mixedwood section of Saskatchewan, growth and yield were reported for poor (site index 17.1 m or 56 ft), average (site index 21.9 m or 72 ft), and good (site index 26.8 m or 88 ft) sites *(84)*. The Saskatchewan data are summarized in table 3.

Mean annual increments of 6.3 to 7.0 m^3/ha (90 to 100 ft^3/acre) have been attained on the best loam soils, and the highest site index 36.6 m (120 ft) is for British Columbia white spruce *(61)*. Site indices for the Lake States *(14)* are somewhat higher than the best in Saskatchewan *(84)*, but below the best sites in British Columbia.

Table 2—Growth, yield, and selected stand characteristics for well-stocked white spruce stands in Alaska (adapted from *41*)

Site index (base age 100)	Stand density	Basal area	Total volume	Mean annual increment (M.A.I.)[1]	Culmination of M.A.I.
m	*trees/ha*	*m^2/ha*	*m^3/ha*	*m^3/ha*	*yr*
14.9	1,324	22.5	78.1	0.8	150
24.4	1,122	33.1	227.2	2.2	100
30.5	959	40.0	351.3	3.6	80
ft	*trees/acre*	*ft^2/acre*	*ft^3/acre*	*ft^3/acre*	*yr*
49	536	98	1,117	12	150
80	454	144	3,245	31	100
100	388	174	5,018	51	80

[1] Trees larger than 11 cm (4.5 in) in d.b.h.

Table 3—Growth and yield of white spruce in a Mixedwood section of Saskatchewan (adapted from *84*)

Site index (base age 70 at stump)	Stand density	Basal area	Total volume	Mean annual increment (M.A.I.)[1]	Culmination of M.A.I.
m	*trees/ha*	*m^2/ha*	*m^3/ha*	*m^3/ha*	*yr*
17.1	1,063	25.7	179.1	2.0	80
22.9	976	35.8	276.4	3.2	70
26.8	815	45.9	373.8	4.3	70
ft	*trees/acre*	*ft^2/acre*	*ft^3/acre*	*ft^3/acre*	*yr*
56	430	112	2,500	28	80
72	395	156	3,950	45	70
88	330	200	5,340	62	70

[1] Trees larger than 9 cm (3.6 in) in d.b.h.

Biomass production in white spruce is not well documented. In the Yukon Flats Region, AK, a 165-year-old stand with a density of about 975 trees per hectare (394/acre), 63 percent less than 20 cm (8 in) in d.b.h., had a standing crop of 12.61 kg/m^2 (2.58 lb/ft^2). It was 97 percent spruce and 3 percent alder and willow. A 124-year-old stand (maximum tree age) with a density of about 3,460 trees per hectare (1,400/acre), 97 percent less than 10 cm (4 in) in d.b.h., had a standing crop of 4.68 kg/m^2 (0.96 lb/ft^2). It was 91 percent spruce and 9 percent alder and willow. Of a total biomass of 57.13 kg/m^2 (11.70 lb/ft^2), 44 percent was overstory, 34 percent forest floor, and 22 percent roots in a 165-year-old interior Alaska stand *(194)*. Within-tree biomass distribution in two approximately 40-year-old trees (total biomass 25 kg or 55 lb) was foliage, 31 percent; branches, 31 percent; and stem, 38 percent. Proportionally, stem biomass was much higher (59 percent) in a 95-year-old tree with a total weight of 454 kg (1,000 lb) above ground; 21 percent was foliage and 18 percent branches *(80)*. Total biomass in an unthinned white spruce plantation in Ontario has been measured at 13.89 kg/m^2 (2.84 lb/ft^2); 19 percent was in roots, 9 percent foliage, and the remaining 72 percent was in the branches and main stem *(142)*.

Natural stands of white spruce can respond well to cultural practices. Released 71-year-old trees in Maine had a mean annual increase (10-year period) in circumference of 1 cm (0.4 in) compared to 0.6 cm (0.2 in) for control trees *(45)*. Basal area increment in 70-year-old Alaskan spruce for a 5-year period was increased 330 percent by thinning and fertilization, 220 percent by thinning, and 160 percent by fertilization *(157)*. Even old white spruce can respond to release.

The ability to respond is related to type of release and degree of damage sustained during release *(66)*. In Manitoba, diameter increment of spruce of all size classes (ages 10 to 60 years) was doubled by removing competing aspen *(138)*. Spruce having their crowns in contact or immediately below those of aspen can be expected to double their height growth following release. The combined effect of increased diameter increment and height growth can increase spruce volume production by 60 percent.

In unmanaged plantations, the onset of density-dependent mortality is determined by site quality and initial spacing. Yield tables for unmanaged white spruce plantations in Ontario *(143)* indicate that mortality at age 20 years will have occurred at 6,730 trees per hectare (2,722 trees/acre) at site index 15.2 m (50 ft) (base age 50 years). At site index 24.4 m (80 ft), mortality will have occurred at densities of 2,990 trees per hectare (1,210/acre) or more by age 20. At 1,080 trees per hectare (436/acre), predicted mortality begins between 30 and 35 years for site index 24.4 m (80 ft) and 40 and 45 years for site index 21.3 m (70 ft). Total volume production in unthinned plantations in Ontario (table 4) is higher than the production in natural stands in Saskatchewan.

White spruce stands should be maintained at basal areas from 23.0 to 32.1 m^2/ha (100 to 140 ft^2/acre) to provide maximum volume growth and good individual tree development; below these levels, individual tree increment and resistance to some pests are greatly increased, but total volume production is reduced. For the sites studied, maximum mean annual increment occurred at about age 55 in unmanaged plantations; at this age, 10 percent of total volume is lost from competition *(5,9,140,142)*.

Rooting Habit—White spruce is frequently characterized as shallow rooted. This generalization stems, however, from the species' ability to occupy sites where soil conditions limit rooting depth *(148)*; depending on soil conditions, competition, and genetics, different forms of taproots and layered roots do develop *(145,166)*. The adventitious multilayered root systems that develop on floodplains in response to silt deposits are particularly noteworthy. Trees from 2 to 132 years old can grow new roots in this way; the response is probably important for maintaining tree vigor *(77,164)*.

Table 4—Volume of white spruce in unthinned plantations in Ontario (adapted from *121*)

Planting density	Plantation age	Site index at base age 50 years	
		15.2 m or 50 ft	24.4 m or 80 ft
trees/ha	*yr*	*m^3/ha*	
6,714	20	43.3	124.8
	50	275.8	513.0
2,197	20	26.8	86.6
	50	212.5	461.7
1,077	20	19.0	66.3
	50	172.8	430.5
trees/acre	*yr*	*ft^3/acre*	
2,717	20	619	1,783
	50	3,940	7,329
889	20	383	1,237
	50	3,036	6,596
436	20	271	947
	50	2,469	6,150

Depth of rooting in white spruce is commonly between 90 and 120 cm (36 and 48 in), but taproots and sinker roots can descend to a depth of 3 m (10 ft). Eighty-five percent of the root mass was in the top 0.3 m (1 ft) on sites in Ontario, but on the most northern sites, large roots are heavily concentrated within 15 cm (6 in) of the organic-mineral soil interface. Lateral spread of the root system was reported to be as much as 18.5 m (61 ft) on sandy soils in Ontario, and lateral root extension was estimated at 0.3 m (1 ft) per year *(141,145,148)*.

Fine-root production in a Maine plantation was 6990 kg/ha (6,237 lb/acre); 87 percent of this material was located in the top 15 cm (6 in) of soil *(136)*. In an Ontario plantation, fine roots 0.25 cm (0.10 in) in diameter and smaller comprised about 10 percent (2670 kg/ha or 2,382 lb/acre) of the total root biomass *(143)*. Sixty-seven percent of the fine-root production in a mixed spruce-fir stand in British Columbia was in the forest floor and A horizon; the average depth of these horizons was 8.3 cm (3.3 in) *(86)*. Mycorrhizae are an important component of the fine roots *(143)* of most conifer species *(89)*, but only a few of the fungi that form mycorrhizae have been found on white spruce.

Root grafting appears to be fairly common in white spruce. In one study, about 27 percent of the trees had root grafts with other trees *(140,149)*.

Reaction to Competition—White spruce is intermediate in tolerance to shade. It is equally or less tolerant to shade than black or red spruce, hemlock (*Tsuga* spp.), balsam and alpine fir, sugar maple, and beech (*Fagus* spp.). It is more tolerant than aspen, paper birch, and lodgepole pine.

Large numbers of white spruce may become established immediately following disturbance and form even-aged stands. Because seedling and juvenile growth of white spruce is slower than its early successional associates, it remains in the understory for 50 to 70 years *(25,104,160,169)*. Although white spruce survives this period of suppression, growth will be significantly reduced *(139)*. White spruce shows a significant response to release resulting from natural causes or silvicultural treatment; ages of trees exhibiting good growth after release range from very young to 200 or more years *(6,22,45, 139,185)*.

White spruce also forms multi-aged pure stands or is a component of multi-aged, late-succession stands mixed with the true firs, maple, beech, and other species. In such stands, age ranges from 200 to 250 years in Alberta *(25)* and from 300 to 350 years in British Columbia *(104)* and at treeline in northern Alaska *(26)*. Natural stands occurring within relatively small areas can show markedly different age structures depending on age of the site, stand history, soil conditions, and other variables *(83)*. The distribution of ages is not continuous but consists of several groups of ages separated by periods when no white spruce become established.

Damaging Agents—Throughout the range of white spruce, fire has been an important, sometimes dominant factor in forest dynamics *(25,136,162)*. Mature forests are easily destroyed because of their high susceptibility to fire. Under certain circumstances, in unmanaged forests white spruce may be eliminated; the probability increases with latitude because seed years are infrequent and seed quality poor in some years in the north *(136,183)*. During early- and mid-succession, white spruce is more susceptible to fire than aspen, birch, black spruce, and lodgepole pine *(182)*.

Fire frequency, intensity, and severity, and not simply the presence of fire, determine white spruce distribution and growth. Fire frequency may range from 10 years or less to more than 200 years; most commonly, it is from 60 to 200 years. If fires occur at short intervals (less than 40 or 50 years), the source of white spruce seed can be eliminated. The reduction in depth of organic matter depends generally on fire severity and is a critical factor because the organic substrate that remains following fire makes a poor seedbed. In general, even severe fires do not expose mineral soil on more than 40 or 50 percent of a burn, and this area is usually distributed in small patches.

On floodplains in the northwestern part of the range, floods and silt deposits provide a seedbed for germination and seedling establishment. Flooding is detrimental to young seedlings, however, and establishment of spruce stands may be prevented until the flooding frequency declines. Fifty years may be required after initial sandbar formation before sedimentation rate declines enough for white spruce to colonize *(104)*. As much as 20 percent of the seedlings may be killed on moist and wet sites that have been scarified by tractor and bulldozer blade *(94)*.

Slow initial root growth makes young seedlings and transplants particularly susceptible to frost heaving. The severity of damage generally is greatest on fine-textured and wet soils where water is adequate for ice crystal formation in the surface soil. Late fall and winter seeding and spring field planting are best in most cases *(141)*. White spruce roots respond vigorously to pruning *(146)*; spring planting with root pruning is likely to be of some protective value against frost heaving.

Depending on soil texture and drainage, white spruce may be prone to windthrow. Windthrow is common along stand edges and in heavily thinned stands on shallow or poorly drained soils where root systems are surficial. On soils where a strong taproot, strong descending secondary roots, or multi-layered root systems develop, the species is much more windfirm. In mixed stands in which white spruce is overtopped by hardwoods, the leader and upper stem of spruce are frequently damaged by hardwood branches whipping in the wind.

Snow and ice can break up to 70 percent of white spruce in stands and hail can cause defoliation, stem lesions, and leader or terminal bud mortality *(31,52,156)*.

White spruce vegetative and reproductive growth are particularly susceptible to frost damage at the time of flushing *(116,181)*. The risk of frost damage is less for late flushing genotypes *(110,116)*. Damage by fall frost is uncommon but has been observed in 1-year-old seedlings, when plantations heavily damaged by spring frost have responded with regrowth in August. Damage from spring frost is less serious after trees reach from 4 to 6 m (13 to 19 ft) in height. Because the species is so susceptible to frost damage, sites exposed to late spring frost should be avoided in all white spruce regeneration efforts.

Young seedlings are damaged by rodents. The snowshoe hare can be a significant pest, but white spruce is not a preferred animal food *(4,12)*.

Environmental factors such as frost, mammals, birds, insects, and disease reduce the number of cones and the number of dispersed seeds *(101,181)*.

The impact of squirrels can be substantial. In Alaska, they may harvest as much as 90 percent of the cone crop *(144,193)*. Small mammals such as deer mice, red-backed and meadow voles, chipmunks, and shrews can be an important cause of failure of natural regeneration and artificial regeneration by direct seeding. Seed consumption by individual animals can be very high—2,000 white spruce seeds per day for caged animals of the species mentioned—and the population density substantial but highly variable. Estimates range from 7 animals per hectare (3/acre) to as high as 44/ha (18/acre). Even at the low density, the impact on regeneration would be unacceptably high *(126,141)*. The impact on seed varies with the time of seeding: 50 percent for spring-sown seeds as compared to 19 percent or less for winter-sown seeds. Coating seeds with repellent is effective and has little influence on seed germination even when coated seeds have been stored for 5.5 years *(125,127)*.

The impact of birds feeding on seeds is small compared to that of rodents *(126)*, but chickadees, grosbeaks, crossbills, juncos, and sparrows feed on coniferous seeds.

Seed losses from insects can be a serious problem. The spruce cone maggot *(Hylemya (Lasiomma) anthracina)*, the fir coneworm *(Dioryctria abietivorella)*, and the spruce seed moth *(Laspeyresia youngana)* are most important. *Hylemya* leaves the cone in midsummer and, as a result, *Laspeyresia* is blamed for the damage it does; however, where the infestation is severe, *Hylemya* may destroy 100 percent of the seed *(59)*. Damage by *D. abietivorella* is particularly severe in years of heavy cone crops and appears to be found when cones develop in clusters. The following insects also attack seeds and cones but do less damage: the spruce cone axis midge *(Dasineura rachiphaga)*, the spruce seed midge *(Mayetiola carpophaga)*, the seed chalcids *(Megastigmus atedius* and *M. picea)*, the cone cochylid *(Henricus fuscodorsana)*, and the cone moth *(Barbara mappana)* *(59)*. The only disease associated with cone production is the cone rust *Chrysomyxa pirolata* *(151)*. Seeds produced from infected cones are about half the weight but the same size as healthy seeds. Seeds are fragile because seed coats are poorly developed, and seed mortality is almost 100 percent in severely affected cones *(101,151)*. Even if viable seeds are produced, they are not readily dispersed because cone malformation and resinosis prevent efficient opening of the cone scales *(151)*.

White spruce seedlings are affected by disease during the dormant and growing seasons. Snow blight *(Phacidium infestans)* causes damage in nurseries and the field. Various species of *Pythium*, *Rhizoctonia*, *Phytophthora*, and *Fusarium* have been shown to be moderately to highly pathogenic to spruce seedlings in both pre- and post-emergent conditions *(65)*. *Pythium* and *Fusarium* as well as *Epicoccum* and *Phoma* can also injure seedlings in cold storage; many of these damaged seedlings die when they are field planted *(67)*. Nematodes have been shown to cause winterkill and reduce seedling vigor.

Needle and bud rusts are common throughout the range of white spruce. The most important rust causing premature defoliation in Canada is *Chrysomyxa ledicola*. Losses of up to 90 percent of the current year's needles have been observed in Western Canada. Other needle rusts that infect white spruce are *C. weiri*, *C. empetri*, *C. ledi*, and *C. chiogenis*. The witches' broom rust *(C. arctostaphyli)* frequently causes dead branches, abnormally proliferating branches, deformed boles, and reduced growth. A bud rust *(C. woroninii)* is more prevelent in far northern areas and infects seedlings and vegetative and female buds of mature trees *(65,101,195)*.

Stem diseases of white spruce are not of major importance. A canker caused by *Valsa kunzei* has been reported. One of the most conspicuous and common stem and branch deformities is a tumor-like growth of unknown origin. These tumors occur throughout the range and may reach 0.6 to 0.9 m (2 to 3 ft) in diameter. In a small test of grafts of tumored and tumor-free trees, tumor growth was transmitted to some, but not all, ramets in some clones of tumored trees *(44)*.

Root diseases of white spruce affect both seedlings and mature trees. *Inonotus tomentosus* is a major cause of slow decline and death of white spruce in patches of 0.4 ha (1 acre) or more in Saskatchewan. The disease has been called the "stand-opening disease." It develops slowly over a period of 20 to 30 years but the impact can be substantial—87 percent of white spruce in mixed stands either dead or heavily rotted at the butt. Stand openings occur on soils of all textures but rarely on alkaline soils *(174)*. Trees planted in infected areas are also damaged *(175)*. Other root-rot fungi associated with white spruce are *Coniophora puteana*, *Scytinostroma galactinium*, *Pholiota alnicola*, *Polyporus guttulatus*, *P. sulphureus*, and *Phaeolus schweinitzii*.

Trunk rots affecting white spruce include *Haematostereum sanguinolentum*, *Peniophora septentrionalis*, and *Phellinus pini*. These species produce rot development beyond the tree base. *Coniophora puteana*, *Fomitopsis pinicola*, and *Scytinostroma galactinium* are associated only with butt rot. In general, cull percentage in white spruce caused by rot is low, particularly for trees less than

100 to 120 years old. Most trees older than 200 years have significant amounts of rot, however.

Although most spruce species are seriously injured by the European strain of scleroderris canker *(Gremmeniella abietina)*, white spruce suffers only from tip dieback and eventually recovers *(137)*. Dwarf mistletoe *(Arceuthobium pusillum)* is usually associated with black spruce, but it has killed white spruce in Minnesota *(3)*, along the coast of Maine, and in the Maritime Provinces.

White spruce is attacked by a number of bark beetles in the genera *Dendroctonus, Ips, Trypodendron, Dryocoetes, Scolytus, Polygraphus*, and others. Although most of these species attack trees of low vigor, dying trees, windthrows, and slash, the spruce beetle *(Dendroctonus rufipennis)* attacks trees of normal vigor and has killed large areas of white and other spruces. In areas with transition maritime climates, such as western and south-central Alaska, prolonged extreme cold (–40° C or –40° F) kills large numbers of beetles. Where spruce beetle outbreaks are common, resistance of trees is greater in mature stands with stocking levels of 18m^2/ha (80 ft^2/acre) or less because of wide tree spacing and rapid growth *(58)*. Dense stocking contributes to cold soils in the spring and thus tree moisture stress, which predisposes the trees to beetle attack *(57)*. Bark beetles bore or mine in the phloem or inner bark and girdle the tree. Symptoms of beetle attack are pitch flow tubes and fine wood particles on the bark or at the base of the tree. The foliage of the attacked tree changes color and dies, but this may not occur until after the beetle has left the tree. The best method of preventing beetle outbreaks is to remove or destroy desirable habitat such as slash and damaged trees; trees weakened by budworms are particularly susceptible.

Wood-boring insects *(Monochamus* spp., *Tetropium* spp., and *Melanophila* spp.) attack weakened or dead white spruce and are particularly attracted to burned areas. They can attack trees almost before the fire cools. The intensity of attack is determined by the condition of the individual tree *(173)*. Lumber recovery from heavily infested trees declines rapidly because of extensive tunneling.

The spruce budworm *(Choristoneura fumiferana)* and the western spruce budworm *(C. occidentalis)* feed and mine in old foliage, in developing reproductive and vegetative buds, and in new foliage of the expanding shoot. True firs are the principal hosts, but spruces are readily attacked and injured. Budworms are the most destructive conifer defoliators; severe defoliation for 2 years reduces growth, and sustained outbreaks have killed all spruce in some stands *(48,81)*. Plantations are not usually subject to serious damage until they are about 6 m (20 ft) tall *(141)*.

The yellowheaded spruce sawfly *(Pikonema alaskensis)*, another defoliator, is not important in closed stands but can seriously reduce growth or kill plantation-grown trees if defoliation continues for 2 or more years *(141)*. A number of other sawflies including the European spruce sawfly *(Diprion hercyniae)*, also damage the species.

Spruce spider mites *(Oligonychus* spp.) build up in damaging numbers in early spring and summer and sometimes in fall. They are also common on young white spruce plants growing in greenhouses. Their feeding destroys the chlorophyll-bearing cells of the needle surface, causing a bleached look. Continuous attacks weaken and eventually kill the tree *(81)*.

The European spruce needleminer *(Epinotia nanana)* causes unsightly webbing and kills needles on spruces in the Eastern United States. Heavy attacks cause severe defoliation, and weakened trees succumb to secondary pests. Other needleminers of less importance are in the genera *Taniva* and *Pulicalvaria (122)*. Other insects damaging spruce needles include needle worms, loopers, tussock moths, the spruce harlequin, and the spruce bud scale.

The gall-forming adelgids *(Adelges* spp.), of which the eastern spruce gall adelgid *(A. abietus)* is the most prevalent, cause cone-shaped galls on the shoots. Other gall-forming insects belong to the *Pineus* and *Mayetiola* genera *(122)*. Although not important for forest trees, these galls can deform and stunt the growth of seedlings, saplings, and ornamental trees *(48,81)*.

Spruce buds are damaged by bud moths, *Zeiraphera* spp., the bud midge *(Rhabdophaga swainei)*, and bud and twig miners *(Argyresthia* spp.). None of these insects causes serious damage *(122)*, but killing of the terminal leader by *Rhabdophaga* results in multiple leaders and thus poor tree form.

White spruce is considered lightly susceptible to damage by the white pine weevil *(Pissodes strobi)* and certainly is much less damaged than either black or Norway spruce *(Picea abies)*. However, an ecotype of the insect, sometimes called the Engelmann spruce weevil, is an important pest in plantations in interior British Columbia and on natural regeneration in British Columbia and Alberta *(141)*.

Warren's collar weevil *(Hylobius warreni)* does cause appreciable damage on spruce. Small trees may be girdled and killed; on older trees, the wounds are entries for root rots such as *Inonotus tomentosus (122)*. In controlled experiments, 4-year-old white spruce has shown high radio-sensitivity when exposed to chronic gamma irradiation. The trees were most sensitive in mid-July when the central mother-cell zone was enlarging.

Special Uses

White spruce trees yield many useful products *(105,148)*. The manufacture of wood fiber and lumber products is well known and white spruce continues to be one of the most important commercial species in the boreal forest. Less well-known uses of white spruce wood are for house logs, musical instruments, paddles, and various boxes and containers.

Historically, white spruce provided shelter and fuel for both Indians and white settlers of the northern forest. White spruce was the most important species utilized by natives of interior Alaska *(105)*. The wood was used for fuel, but other parts of the tree also had a purpose; bark was used to cover summer dwellings, roots for lashing birchbark baskets and canoes, and boughs for bedding. Spruce pitch (resin) and extracts from boiled needles were used for medicinal purposes *(163)*.

White spruce stands are a source of cover and food for some species of game. Moose and hares frequent these forests but seldom eat white spruce, whereas red squirrels and spruce grouse live in these forests and also consume parts of the tree. Prey species (furbearers) such as marten, wolverine, lynx, wolves, and others utilize these forests.

White spruce forests have significant value in maintaining soil stability and watershed values and for recreation. White spruce can be planted as an ornamental and is used in shelterbelts.

Genetics

Population Differences

White spruce is highly variable over its range; the variation pattern is clinal and generally follows the latitudinal and altitudinal gradients. As an example, southern provenances are the fastest growing and the latest flushing when tested near the southern edge of the range; Alaskan trees are dwarfs and are susceptible to spring frost because they flush early. Soil-related adaptive variation has been demonstrated, and variation in germination temperature requirements have also been described *(117)*. Because the species shows such strong adaptive affinity to local environments, seed collection and seed and seedling distribution must adhere to seed zoning and seed transfer rules.

Variation in monoterpenes, DNA content, and taxonomic characteristics suggest two major populations—one in the East, east of longitude 95° W., and another in the West. Further subdivision of these populations must await new research *(117)*. Two high-yielding provenances have been identified. In the East, a source centered around Beachburg and Douglas in the Ottawa River Valley about 97 km (60 mi) northwest of Ottawa has proven superior in the Lake States, New England, and southern portions of the range in eastern Canada *(96)*. In the West, the Birch Island provenance (lat. 51° 37′ N., long. 119° 51′ W., elev. 425 m (1,400 ft)) has been exceptional. In coastal nurseries, it will grow as fast as Sitka spruce.

Provisional seed zones have been summarized for Canada *(141)* and are being developed for Alaska. In the Lake States, general zones have been developed, and superior and also inferior seed sources identified *(113,135)*. Tentative seed transfer rules have been suggested for British Columbia. They limit altitudinal movement to 150 m (500 ft) and suggest that high-elevation spruce provenances from southern latitudes can be moved 2 to 3 degrees of latitude. They also warn that a transfer north of more than 3 degrees will probably result in a detrimental silvicultural effect in southern provenances from low elevations *(131)*. Analysis of enzyme patterns is providing new information on population structure that can be used for improving and refining seed management practices for reforestation *(2,17,20)*.

Hybrids between provenances have been tested on a small scale with promising preliminary results *(179)*. Constructing seed orchards of mixed provenances or of selected alien trees and selection from the local provenance could be an inexpensive approach to increasing yields.

Individual Tree Differences

Genetic variation at the individual tree or family level has implications of silvicultural importance. Large differences exist among families representing individual trees within a stand. For example, in a study representing six families from each of seven stands located over a 3550 km² (1,370 mi²) area in the Ottawa River Valley, no differences could be demonstrated. The best of all the families was 28 percent taller than the family mean height *(28)*. This indicates that substantial genetic improvement can be achieved through mass selection and low-cost tree improvement programs.

The general feasibility of phenotypic selection in white spruce has been demonstrated *(74)*. Seed trees, therefore, should be selected for rapid growth and other desirable characteristics; in even-aged stands on uniform sites, this approach may lead to limited improvement. Similarly, the slower growing, poorer trees should consistently be removed in thinning.

Juvenile selections made in the nursery based on height growth maintain superior growth until age 22 and their phenotypic growth superiority probably reflects genetic superiority *(111)*. Silvicultural implications are that extra large seedlings should never be culled merely because "they are too large for the planting machine." On the contrary, they should be given extra care to assure survival and immediate resumption of growth without "check." Furthermore, propagules of such juvenile selections used in intensively managed plantations may lead to immediate yield improvement *(115)*.

Selfing results in serious losses in vigor and lowered survival. Height growth reduction as great as 33 percent has been reported *(180)*. Not much is known about natural selfing in white spruce, but relatedness between individuals within a stand has been demonstrated; it manifests itself in terms of reduced seedset and slower early growth *(19)*. These relations have several implications: (a) culling small plants in the nursery is desirable because it may eliminate genetically inferior inbred seedlings; (b) collecting seed from isolated trees is undesirable because they are likely to produce a high proportion of empty seeds and weak seedlings; and (c) collecting seed in stands likely to represent progeny of one or a few parent trees, as in old field stands, may lead to a degree of inbreeding.

Races and Hybrids

No races of white spruce are recognized, but four varieties have been named: *Picea glauca, Picea glauca* var. *albertiana, Picea glauca* var. *densata,* and *Picea glauca* var. *porsildii*. It seems unnecessary to distinguish varieties, however *(23,96)*.

White and Engelmann spruce are sympatric over large areas in British Columbia, Montana, and Wyoming. White spruce predominates at lower elevations (up to 1520 m or 5,000 ft), and Engelmann spruce predominates at higher elevations (over 1830 m or 6,000 ft). The intervening slopes support a swarm of hybrids between the two species; these hybrids are the type that gave rise to the so-called variety *albertiana*.

Sitka and white spruce overlap in northwestern British Columbia and areas in Alaska. The hybrid *Picea* × *lutzi* Little occurs where the species are sympatric. The population in Skeena Valley has been studied in some detail. It represents a gradual transition from Sitka to white spruce, a hybrid swarm resulting from introgressive hybridization *(20,130)*.

Natural hybrids between black and white spruce are rare along the southern edge of the species' range, undoubtedly because female receptivity of the two species is asynchronous. A single occurrence from Minnesota has been described *(97)* and its hybrid origin definitely established *(129)*. To the north, they are more common; intermediate types occur north of latitude 57° N. along the Alaskan highway in British Columbia *(130)*. The hybrids have also been found along the treeline in the forest tundra *(93)*.

Many artificial hybrids have been produced *(75,117)*; a few show some promise, but none has achieved commercial importance.

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Picea mariana (Mill.) B.S.P. Black Spruce

Pinaceae Pine family

Leslie A. Viereck and William F. Johnston

Black spruce *(Picea mariana)*, also called bog spruce, swamp spruce, and shortleaf black spruce, is a wide-ranging, abundant conifer of the northern parts of North America. Its wood is yellow-white in color, relatively light in weight, and strong. Black spruce is the most important pulpwood species of Canada and is also commercially important in the Lake States, especially Minnesota.

Habitat

Native Range

Black spruce (fig. 1) ranges in a broad band from northern Massachusetts to northern Labrador on the Atlantic coast, west across Canada to the west coast of Alaska. Its southern limits consist of isolated patches in northern New Jersey, western Connecticut, Pennsylvania, southern Michigan, southern Wisconsin, southern Minnesota, and southern Manitoba; west across south-central Saskatchewan, Alberta, and central British Columbia. Its northern limit across Canada and Alaska is about that of the northern tree line, although it alternates with white spruce *(Picea glauca)*, tamarack *(Larix laricina)*, and balsam poplar *(Populus balsamifera)* as the tree line species at different points.

The commercial range of black spruce is considerably less than its geographic range.

Climate

The climate for black spruce can be characterized as cold with a moisture regime varying from humid to dry subhumid. Mean annual temperatures range from 7° C (45° F) in the southern areas to -11° C (13° F) near tree line in central and western Canada. Average January temperatures range from -30° C (-22° F) in northwestern Canada and Alaska to -6° C (21° F) at the southeastern edge of its range. Average July temperatures range from 16° to 24° C (60° to 76° F) in the main part of the range of black spruce and from 10° to 27° C (50° to 80° F) in extreme locations. The extreme low temperatures range from -62° to -34° C (-79° to -30° F), the highs from 27° to 41° C (80° to 105° F).

Annual precipitation decreases from east to west. In the maritime provinces, it may be as high as 1520 mm (60 in) and in western Alaska as low as 150 mm (6 in), but annual precipitation ranges from 380 to 760 mm (15 to 30 in) in most of the black spruce range. Much of the precipitation is snowfall—from 500 cm (200 in) in eastern Canada to 100 cm (40 in) in western Canada and central Alaska. Mean snow depths are 50 to 75 cm (20 to 30 in) over most of the range but may be more than 100 cm (40 in) in parts of Quebec and Labrador, where snow may persist into late May or early June.

Maximum length of days during the growing season varies from continuous north of the Arctic Circle to about 16 hours near the southern limits of the range. The frost-free period varies from 140 days in the southeastern portions of the range to 60 days or less near tree line.

Soils and Topography

Black spruce (fig. 2) usually grows on wet organic soils, but productive stands are found on a variety of soil types from deep humus through clays, loams, sands, coarse till, boulder pavements, and shallow soil mantles over bedrock. In the Lake States and adjacent Canadian provinces, it grows on soils of the order Histosols: peat bogs and swamps that have formed on old glacial lakebeds and in muck-filled seepages on peat deposits that range in thickness from 0.5 to 6 m (20 in to 20 ft). The most productive black spruce stands are on dark brown to blackish peats, which usually have a considerable amount of decayed woody material. Stands of low productivity are usually found on thick deposits of partially decomposed sphagnum peat.

In central Canada, upland stands tend to be of higher quality than the lowland peat stands. Here, podzolic soils of the order Spodosols and gley soils of the order Inceptisols are common on gentle slopes underlain by clay-loam or clays that have been derived from glacial tills. Many of these clay soils are derived from calcareous materials and are neutral to slightly alkaline in the B or C horizons. The most productive black spruce stands are found on the better drained sites such as sandy glacial deposits, river terraces, and outwash plains of the order Entisols, usually in association with hardwood species.

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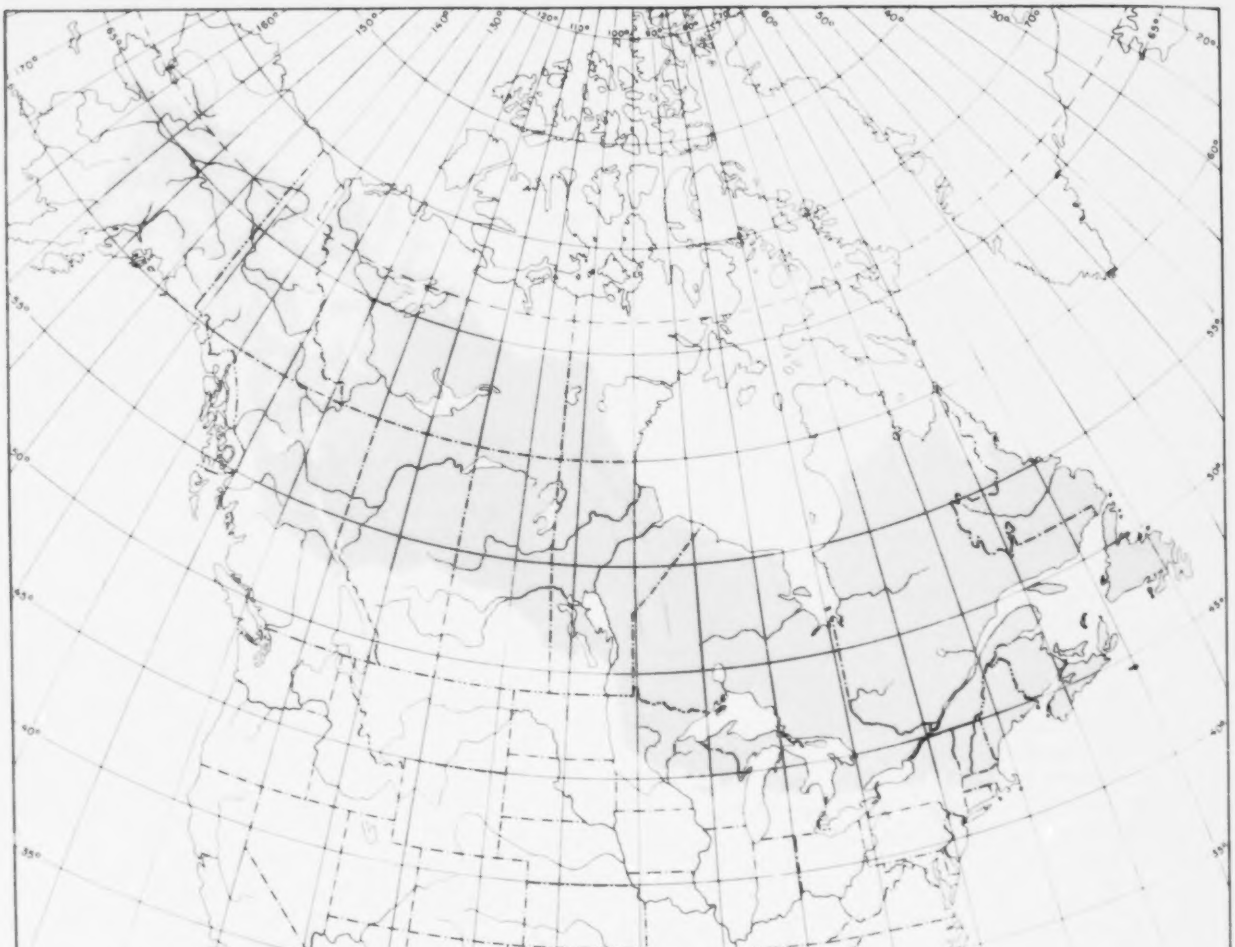
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Figure 1—*The native range of black spruce.*

Figure 2—*Black spruce stand in a swamp in Minnesota.*

In the north, black spruce sites are commonly underlain by permafrost (perennially frozen soils). Black spruce seems to be the tree species best adapted to growing on permafrost soils because of its shallow rooting habit. Often the annual thaw depth (active zone) may be as little as 40 cm (16 in). In northwestern Canada, black spruce often grows in alternating organic and mineral soil layers, on hummocklike mounds that overlie the permafrost *(57)*. In central Alaska, black spruce is found on permafrost sites of shallow wind-deposited loess and on old river terraces. At tree line, it is often found on shallow, poorly developed mineral soils. On most black spruce sites on permafrost, wildfire results in a temporary increase in the thaw depth.

Black spruce is found from sea level in eastern and northern Canada and western Alaska to 1830 m (6,000 ft) in northern Alberta. It is considered to be a tree of interior lowlands, however, and usually grows at between 150 and 760 m (500 and 2,500 ft). In the mountains of Alaska, Yukon Territory, and Northwest Territories, it is often the tree line species at elevations of 300 to 1220 m (1,000 to 4,000 ft). Local topography and drainage seem to be more important than elevation in determining the range of black spruce.

Associated Forest Cover

Black spruce most commonly grows as pure stands on organic soils and as mixed stands on mineral soil sites. It is a major component of forest types with white spruce, balsam fir *(Abies balsamea)*, jack pine *(Pinus banksiana)*, and tamarack and also grows in association with paper birch *(Betula papyrifera)*, lodgepole pine *(P. contorta)*, quaking aspen *(Populus tremuloides)*, balsam poplar, northern white-cedar *(Thuja occidentalis)*, black ash *(Fraxinus nigra)*, American elm *(Ulmus americana)*, and red maple *(Acer rubrum)*. In the southern parts of its range, black spruce is commonly found in mixed stands with several species, especially northern white-cedar, white spruce, balsam fir, and tamarack. In the main part of its range, it is commonly associated with white spruce, quaking aspen, balsam fir, paper birch, and tamarack. Jack pine is a common associate on dry sites. At the northern and northwestern limits of the range, pure stands are common, but black spruce is also found associated with paper birch, quaking aspen, white spruce, and tamarack.

Because of its broad distribution and varying ecological site characteristics, the Black Spruce forest cover type (Society of American Foresters Type 12, eastern, and 204, western) *(11)* has been divided into six subtypes: (a) black spruce-feathermoss, most common in the southern and central boreal forest; (b) black spruce-lichen, most abundant near the northern limit of the boreal forest; (c) black spruce-dwarf shrub, in the southern and central portions of the boreal forest; (d) black spruce-sphagnum, on wet soils; (e) black spruce-speckled alder *(Alnus rugosa)*, on waterlogged soils with standing or slowly flowing water; and (f) black spruce-sedge, on peatlands with minerally enriched moving water. Black spruce is also a major component of cover types Black Spruce–Tamarack (Type 13); Black Spruce–White Spruce (Type 253); and Black Spruce–Paper Birch (Type 254).

One of the most conspicuous aspects of many black spruce stands is a nearly continuous ground cover of feathermosses *(Hylocomium splendens, Pleurozium schreberi,* and *Ptilium crista-castrensis)* and sphagnum mosses *(Sphagnum* spp.). On some sites, the moss layer is replaced by nearly continuous mats of lichens, primarily species of *Cladonia*; this is especially typical of open stands in northern areas where the open lichen woodland is a common vegetation type.

The shrubs associated with black spruce change gradually from east to west. Dominant shrubs in the eastern range include mountain maple *(Acer spicatum)*, beaked hazel *(Corylus cornuta)*, speckled alder, red-osier dogwood *(Cornus stolonifera)*, and red raspberry *(Rubus idaeus)* on better sites; and low birch *(Betula pumila)*, bog birch *(B. glandulosa)*, bog-rosemary *(Andromeda glaucophylla)*, lambkill *(Kal-*

mia angustifolia), Labrador-tea *(Ledum groenlandicum)*, leatherleaf *(Chamaedaphne calyculata)*, and bog-laurel *(Kalmia polifolia)* on the less productive peatlands. In the western part of the range, littletree willow *(Salix arbusculoides)*, grayleaf willow *(S. glauca)*, Bebb willow *(S. bebbiana)*, prickly rose *(Rosa acicularis)*, American green alder *(Alnus crispa)*, Labrador-tea, bog blueberry *(Vaccinium uliginosum)*, and mountain cranberry *(Vaccinium vitis-idaea)* are the most important shrubs. The most important herbs, found over most of the range, are panicle bluebells *(Mertensia paniculata)*, fireweed *(Epilobium angustifolium)*, one-sided pyrola *(Pyrola secunda)*, twinflower *(Linnaea borealis)*, bunchberry *(Cornus canadensis)*, wild sarsaparilla *(Aralia nudicaulis)*, false lily-of-the-valley *(Maianthemum canadense)*, starflower *(Trientalis borealis)*, bluejoint reedgrass *(Calamagrostis canadensis)*, and sheathed cottonsedge *(Eriophorum vaginatum)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Black spruce is monoecious. Female flowers (ovulate strobili), produced in the upper meter of the crown, are usually erect, cylindrical, and green or purplish. At the time of fertilization, the female conelet is about 15 to 25 mm (0.6 to 1.0 in) in length. The male flowers (staminate strobili), produced on the outer branches of the crown below the zone of female flowers, are ovate, 12 to 20 mm (0.5 to 0.8 in) long and dark red to purplish during expansion. The pollen sacs are yellow, and after pollen dispersal the staminate flowers appear yellowish brown. A few cones may be produced after 10 years *(2)*, but the main cone-bearing age of black spruce is from 30 to 250, with maximum production between 100 and 200 years *(6)*.

The flower buds formed by early August develop rapidly the following spring. Female flowers are receptive and pollen is shed in late May or early June in southern areas of the range and 1 to 2 weeks later in the north. The female conelets then develop rapidly, and at maturity the cones are 1 to 4 cm (0.4 to 1.6 in) long.

Seed Production and Dissemination—Black spruce seeds mature 3 months after pollination, in late August or early September. Some are produced almost every year, but heavy seed years occur at intervals of 2 to 6 years and peak crops every 4 years over most of the range. Good seed years may be less frequent in the north; vegetative reproduction of clonal populations occurs at the northern limit of black spruce in Canada *(36)*.

The cones of black spruce remain partially closed and disperse seed for several years, providing an adequate supply of seeds to reproduce the stand whenever fire occurs. Both the number and viability of the seeds decline rapidly, but some viable seeds may remain in the cones for as long as 25 years *(15)*. In Minnesota, 1-year-old cones contained an average of 50 seeds; 7-year-old cones, 10 seeds; and 19-year-old cones, only 1 or 2 seeds *(50)*. In Newfoundland, the number of seeds per cone was greatly reduced in 4 years (3.7 seeds per cone), but seed germination remained high (above 90 percent) for 12 years and then declined rapidly in older seeds *(44)*.

Black spruce seeds are dispersed throughout the year, but dispersal is highest in the spring and lowest in the fall *(16)*. Fires open the cones and accelerate seed fall for periods of 60 days *(55)* to 2 to 3 years; the effect apparently varies with fire intensity.

The average annual seedfall is about 490,000/ha (200,000/acre) for Minnesota *(26)* and substantially higher for Ontario—2,450,000 to 4,180,000/ha (990,000 to 1,692,000/acre) *(15)*. A maximum of 12,720,000 seeds per hectare (5,148,000/acre) has been reported from Ontario *(29)*. In northern areas, even near tree line, amounts of seed are within the range of those from southern areas, with annual amounts from 590,000 to 1,300,000/ha (240,000 to 528,000/acre) reported from Inuvik in Northwest Territories *(6)* and 850,000/ha (344,000/acre) from central Alaska *(49)*.

Black spruce has the smallest seed produced by any spruce in North America, averaging 890,000/kg (404,000/lb). Despite their light weight and relatively large wings, the seeds are not commonly dispersed over long distances. Seed dispersal, primarily by wind, is effective up to 79 m (260 ft) from the windward edge of a mature stand *(27)*.

Seedling Development—Sphagnum mosses provide a continuously moist seedbed in many areas, but growth of black spruce seedlings may be slow in sphagnum moss because of a poor supply of nutrients *(23,24)*, and they may not be able to keep ahead of some fast-growing sphagnum species that eventually overtop them. Feathermosses may provide a suitable seedbed during wet years, but they are unreliable and usually dry out before penetration by the seedling root occurs. Moist mineral soils usually provide good seedbeds for black spruce, but exposed mineral soil may be too waterlogged or subject to frost heaving in some low-lying areas *(23)*.

Fires that completely remove the surface organic layer usually provide good seedbeds for black spruce. Slash removal by broadcast burning or full-tree skidding is also beneficial *(8,26)*. Seedling mortality seems to be highest on burned duff and lowest on some moss and mineral soil surfaces with an adequate moisture regime.

Seedbed scarification increases stocking. Under optimal climatic conditions, direct seeding on these scarified surfaces results in seedlings representing 10 to 30 percent of the sown seed *(25,56)*. A sowing of 79,000 seeds per hectare (32,000/acre) should result in at least 60 percent milacre (4.05 m^2 or 43.56 ft^2) stocking of seedlings, which is considered satisfactory *(26)*. Spring sowing results in the best germination and survival, and viability is drastically lowered if germination does not occur during the same year *(13,56)*. Germination is epigeal *(42)*.

Nursery-grown transplants (2-2) survive better, grow faster, and are more economical than seedlings (3-0) when black spruce plantations are established *(34,35)*. Average initial height growth of black spruce seedlings varies from 2.5 cm (1 in) per year on moss to 15 cm (6 in) per year on some mineral soil substrates, but annual growth may be as low as 5 mm (0.2 in).

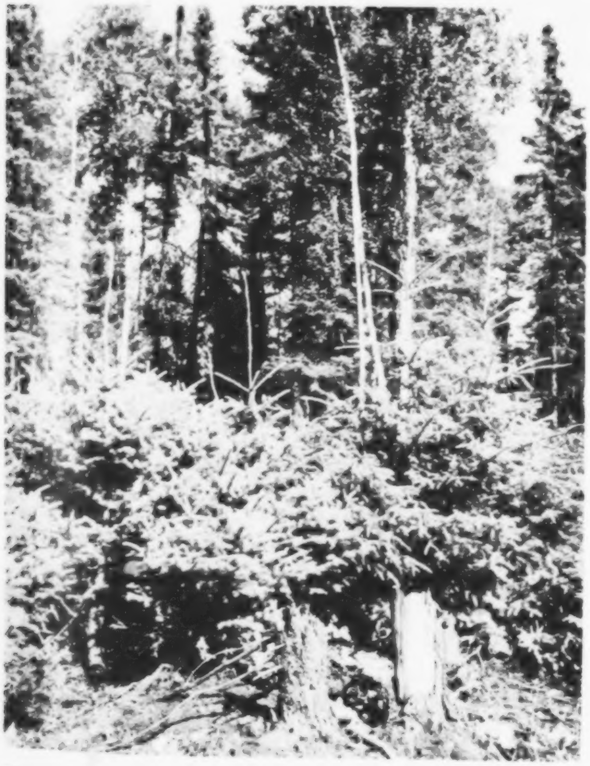

Figure 3—*Vegetatively reproduced layering of black spruce; the "mother" trees were damaged by logging 6 years earlier.*

Vegetative Reproduction—Layering (fig. 3) is an important means of reproduction in black spruce on some sites, especially where rapidly growing mosses cover the lower branches of the slow-growing seedlings and saplings *(45)*. Layerings from the lower branches develop most abundantly in the more open-grown, poorer stands and less frequently in dense, productive stands. Layering is common in black spruce growing at tree line, probably as a result of depression of the lower branches by snow, and accounts for the presence of "candelabrum" spruce, a circular clump originating from one individual with the tallest tree in the center. Layering is also common in black spruce/speckled alder communities on organic soils but is rare in well-stocked black spruce/Labrador-tea stands *(45)*. The trees established from layerings constitute advance growth on some sites and are particularly important where logging disturbance is light.

Black spruce may reproduce from shoots originating from roots *(12)*, but this is uncommon. Cuttings from black spruce seedlings can be rooted successfully with periodic misting but without application of auxins *(3)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Under normal unmanaged conditions, black spruce (fig. 4) at maturity averages 12 to 20 m (40 to 65 ft) tall and about 23 cm (9 in) in d.b.h. on good sites; 8 to 12 m (25 to 40 ft) and about 13 cm (5 in) in d.b.h. on poor sites. Extreme sizes vary from semiprostrate shrubs or trees to 3 to 6 m (10 to 20 ft) tall and 3 to 5 cm (1 to 2 in) in d.b.h. in the far north to occasional individuals that are about 27 m (90 ft) tall and 46 cm (18 in) in d.b.h. in the Ontario Clay Belt *(12,50)*. Average maximum age is about 200 years, but ages up to 280 years have been reported.

Volumes of 196 m^3/ha (2,800 $ft^3/acre$) are common in 80- to 100-year-old stands on the best peatlands and good upland sites in southern Canada and the Lake States *(12)*. One unmanaged stand had a total volume of 492 m^3/ha (7,024 $ft^3/acre$) and a basal area of 53.5 m^2/ha (233 $ft^2/acre$) when it was slightly more than 100 years old.

Regional differences in the site index of black spruce are apparently related to climatic factors, whereas differences within regions are associated with soil moisture and nutrients. The moisture-aeration regime influences growth more than the

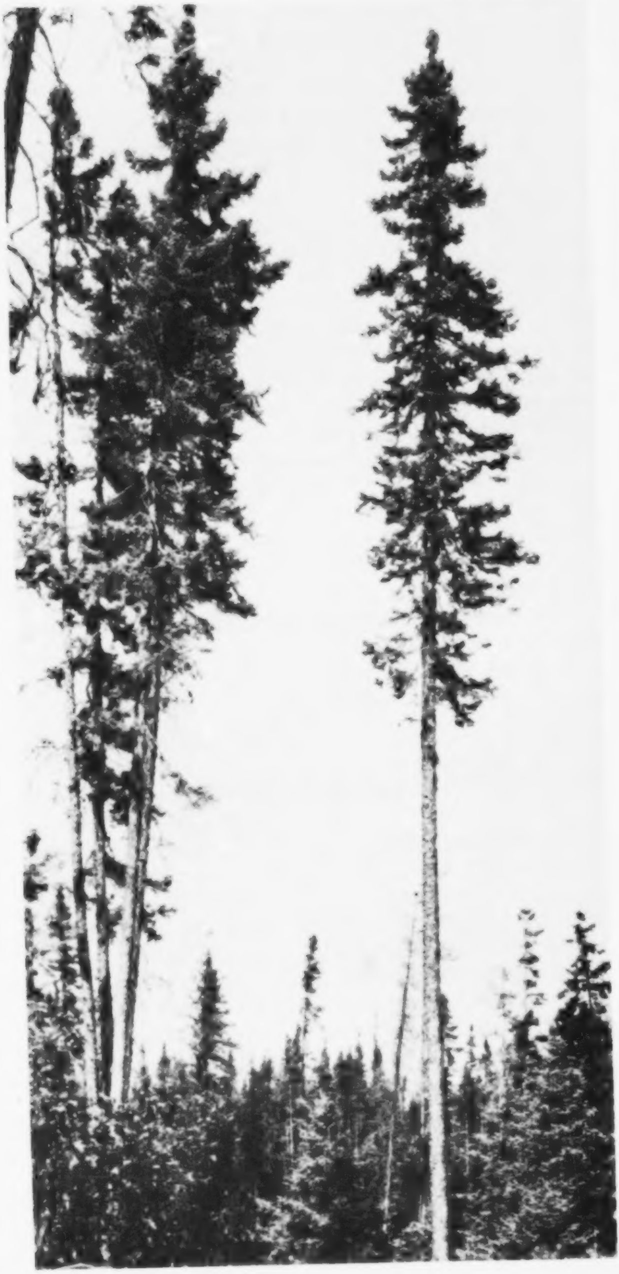

Figure 4—*A 120-year-old black spruce (center). It is 25 cm (10 in) in d.b.h. and 20 m (65 ft) tall.*

nutrient regime *(22)*. Within peatlands, water chemistry—as determined by water sources and movement—seems to be the principal factor influencing site quality *(19)*.

Table 1—Merchantable yields of 120-year-old black spruce stands in Ontario for trees 10 cm (4 in) d.b.h. and larger (adapted from *10*).

Characteristic	Stocking[1] at age 30	Site index at base age 50 years		
		12.5 m or 41 ft	10.7 m or 35 ft	8.2 m or 27 ft
Average height, m	Full	17	14	11
	Half	17	14	11
Average d.b.h., cm	Full	19	13	11
	Half	20	15	12
Trees per hectare	Full	1,520	2,480	1,490
	Half	1,110	1,880	1,780
Basal area, m²/ha	Full	42	35	15
	Half	36	33	19
Volume, m³/ha	Full	298	212	74
	Half	260	202	94
Average height, ft	Full	57	47	37
	Half	57	47	37
Average d.b.h., in	Full	7.4	5.3	4.4
	Half	8.0	5.9	4.6
Trees per acre	Full	615	1,005	605
	Half	450	760	720
Basal area ft²/acre	Full	181	152	65
	Half	158	145	83
Volume, ft³/acre	Full	4,260	3,030	1,050
	Half	3,710	2,880	1,350

[1] "Full" refers to a basal area—for trees 2.5 cm (1 in) in d.b.h. and larger—of 18.4 m²/ha (80 ft²/acre) on site index 12.5 m (41 ft) good site; medium site, 13.8 m²/ha (60 ft²/acre) on site index 10.7 m (35 ft); and 4.6 m²/ha (20 ft²/acre) on site index 8.2 m (27 ft) poor site. "Half" refers to one-half of the respective basal areas used for full stocking.

Black spruce site index curves differ among regions and substrates. For example, the curves are lower at older ages in Newfoundland than in continental Ontario and Quebec. In Ontario, the height-growth patterns of black spruce are different for peatland and upland stands, particularly for site indexes less than 8 m (26 ft) at 50 years and stands older than 80 years *(38)*.

Variable-density yield tables—for stands of various stocking levels—provide better estimates of black spruce growth than normal and empirical yield tables in Ontario *(10)*. They show that both site and stocking influence tree size and volume production. Good sites can grow larger trees than poor sites, whereas stocking has an adverse effect on average d.b.h. and no effect on average height. Merchantable volume, however, increases with stocking except on poor sites (table 1). Variable-density yield tables are also available for black spruce stands in Minnesota *(39)*.

Normal yield tables show that rotation age increases as site quality decreases. They also show that the corresponding merchantable volume and mean annual increment decrease greatly from good to poor sites. Averages for black spruce stands of three site classes in the boreal forest of Canada (*5*, p. 50,91,155,186) are as follows:

	Good	Medium	Poor
Rotation age, yr	95	113	132
Merchantable volume, m³/ha	218	160	101
Mean annual increment, m³/ha	2.3	1.4	0.8
Merchantable volume, ft³/acre	3,110	2,285	1,440
Mean annual increment, ft³/acre	33	20	11

Rotation age is the age at which the mean annual increment of merchantable volume culminates and hence yields the most material per unit area per annum.

Little is known about the growth and yield of uneven-aged stands, but they apparently grow more slowly and have lower volumes than even-aged stands (*17*).

Black spruce plantations reach heights of 1.5 to 4.0 m (5 to 13 ft) 10 years after planting (*2,34*). A 40-year-old plantation in Minnesota, planted at a 1.2- by 1.2-m (4- by 4-ft) spacing, was 13.3 m (43.6 ft) tall and had a basal area of 32.8 m²/ha (143 ft²/acre) (*43*). On rich sites in New Brunswick, extensive fast-growing plantations of black spruce have been established for 45-year rotations because the species has good potential height growth and is resistant to spruce budworm.

In experimental studies, fertilization with nitrogen and phosphorus generally results in increased growth in 60- to 90-year-old stands on upland boreal sites (*48*). The best response to fertilization apparently occurs in stands of low vigor (*33,53*). For example, fertilization (with nitrogen and phosphorus combined) may convert some marginally nonproductive muskeg stands of black spruce into commercial forest stands (*1*). Benefits from fertilization will probably be greatest in thinned stands (*51*).

Drainage may increase the growth and yield of black spruce, but maximum response on peatlands and other wet sites will probably also require fertilization and (in dense stands) thinning. Full-tree harvesting will probably not reduce future productivity, except on sites of marginal fertility (*52*).

Rooting Habit—Although some black spruce roots may penetrate to 60 cm (24 in), most spread laterally at the moss-humus interface. The bulk of the root biomass is in the upper 20 cm (8 in) of the organic horizons. In areas with rapidly accumulating organic layers, several sets of progressively younger roots may develop adventitiously. These new roots may grow as fast as 1 m (3 ft) per year and as much as 4.6 m (15 ft) in 8 to 9 years (*2*).

Reaction to Competition—Black spruce is classed as tolerant of shade but is less tolerant than balsam fir and northern white-cedar, two common competitors in the eastern part of its range. Seedlings (and apparently layerings) develop in as little as 10 percent of full light intensity, but survival and growth are much better in the open (*12*). The maximum overstory basal area that can be tolerated without serious loss of seedling vigor is probably 9 to 11 m²/ha (40 to 50 ft²/acre).

Aerial spraying of selective herbicides such as 2, 4-D usually results in effective release of black spruce in brushy stands (*26,50*). Released trees, however, apparently do not increase growth for about 2 years, and complete release can result in winter drying. Applying pellets of the nonselective herbicide picloram to speckled alder clumps seems to control regrowth longer than 2,4-D but can damage associated black spruce even on well-drained soils (*40*). Although quite expensive, recently introduced selective herbicides such as glyphosate and hexazinone are also registered for release of spruce. Directions on all herbicide labels should be followed carefully and pertinent precautions heeded.

In spruce-fir stands, mature black spruce apparently responds better to release than white spruce and subalpine fir (*Abies lasiocarpa*); its diameter increment increases by several times (*9*). Many intermediate and suppressed black spruce in swamp stands, however, die after heavy cutting (*21*).

Black spruce has less ability than white spruce to overcome stagnation in even-aged stands because it develops a smaller range of crown classes. Heavy thinning in dense, middle-aged stands increases diameter increment but often decreases volume increment, probably because the site is not fully utilized (*47*).

Black spruce is often a postfire pioneer on both uplands and peatlands, and fire usually results in the immediate reestablishment of black spruce as long as a seed source is available. Black spruce often dominates fire-prone areas, such as upland ridges, because it produces seed at an early age (*20*). It also becomes dominant on poor peatland (bog) sites where it has little competition. Tamarack and black spruce are the first trees to invade the sedge mat in filled-lake bogs.

Postfire stands of black spruce are generally even aged. Uneven- to all-aged stands are almost absent in virgin forests because wildfires have been frequent and extensive enough to prevent their development on most sites. Such stands are common on bogs and muskegs, however, where the average interval between fires is probably longer than on uplands. Closed stands that escape fire for more than 100 years usually become uneven aged when black spruce layerings fill the gaps created by deterioration of the overstory *(17)*.

Black spruce grows more slowly than many of the trees and shrubs with which it is associated. Thus, it encounters substantial competition where these species are abundant, particularly when they reproduce from sprouts or suckers rather than from seed. Black spruce is fairly common as an understory tree in jack pine and lodgepole pine stands on dry sites, and succeeds the pines in the absence of fire or harvesting *(12)*. Various mixtures of black spruce, white spruce, and balsam fir—plus northern white-cedar south of the boreal forest—eventually form the main stand on most well-drained sites supporting quaking aspen, paper birch, or balsam poplar. On the better peatland sites, black spruce is often overtopped by quaking aspen, paper birch, tamarack, black ash, or red maple for many years before it becomes dominant. Over much of its range, it is eventually succeeded by balsam fir and, to a lesser extent, northern white-cedar if undisturbed by fire *(17)*.

Black spruce does not compete successfully with balsam fir, northern white-cedar, red maple, balsam poplar, and black ash after cutting in mixed stands on good peatland sites *(12)*. Similarly, harvesting or other disturbances on well-drained sites often lead to high proportions of balsam fir, paper birch, quaking aspen, and balsam poplar, or shrubs *(50)*. Speckled alder is a strong competitor following harvesting on good peatland sites. The spruce, however, is generally able to grow through the alder canopy after several years *(50)*. In Newfoundland and parts of Quebec, there has been extensive conversion of black spruce stands to heathland, dominated by lambkill and Labrador-tea, following repeated fires.

Clearcutting in strips or patches is generally considered to be the best silvicultural system for managing black spruce *(21,26,50)*. Satisfactory reestablishment of black spruce after clearcutting, however, requires an adequate source of reproduction and often some kind of site preparation, such as slash disposal. Uneven- or all-aged management is best applied on poor sites where stands are windfirm and have abundant layering *(27)*.

Damaging Agents—Eastern dwarfmistletoe *(Arceuthobium pusillum)* is a destructive disease of black spruce in the Lake States and eastern Canada, but it appears less often in the West and is completely absent in northwestern Canada and Alaska *(18)*. In most areas, infection by mistletoe results in reduced vigor, clumped branches (witches' brooms), and deformed trees; but in some stands it may kill many trees. Successful control is possible by incorporating control methods in the silvicultural management *(37)*.

Several rusts of the genus *Chrysomyxa* infect both the buds and needles of black spruce. The infection usually remains at low levels but occasionally becomes epidemic and causes defoliation, reduced vigor, and even death of seedlings, saplings, and trees. The cone rust *(Chrysomyxa pirolata)* often results in greatly reduced seed production but does not kill the tree.

Other diseases of black spruce include a needle cast fungus *(Lophodermium* spp.), which may cause defoliation and death in local areas; a yellow rust witches' broom *(Chrysomyxa arctostaphyli)*; and a snow blight *(Lophophacidium hyperboreum)*, which may cause extensive damage to black spruce growing in nurseries or young regeneration in the field.

White pocket rots of roots and stems, most commonly *Inonotus tomentosus*, occur in black spruce and may cause significant damage in some upland stands *(4,54)*.

The spruce budworm *(Choristoneura fumiferana)* is one of the insects most damaging to black spruce, even though black spruce is less susceptible than red spruce *(Picea rubens)*, white spruce, and balsam fir. Budworm defoliation for several years in succession may result in moderate to severe mortality. The budworm and several other insects often cause serious damage to the flowers or cones, resulting in reduced seed crops *(50)*.

The European spruce sawfly *(Diprion hercyniae)* is an important pest in eastern Canada but has not invaded western portions of the range. The yellowheaded spruce sawfly *(Pikonema alaskensis)* and greenheaded spruce sawfly *(P. dimmockii)* occasionally defoliate black spruce but seldom cause serious damage over large areas. Occasionally, a buildup in populations of the spruce beetle *(Dendroctonus rufipennis)* in white spruce leads to invasion and death of black spruce, usually where the two species are growing together. The spruce bud midge *(Rhabdophaga swainei)* may affect height growth in black spruce under some conditions *(7)*. *Monochamus* wood borers have been known to kill considerable numbers of trees in areas adjacent to strip cuts as a result of initial buildup of populations in logging slash *(50)*.

Snowshoe hare may cause extensive damage to seedlings and saplings when populations of hare are high. Red squirrels gather cones in large quantities and give a peculiar clumped appearance to the top of the tree. Squirrels and microtines may consume a large percentage of the seed supply in some areas during poor seed years.

Black spruce tops are often broken at a height of 3 to 6 m (10 to 20 ft) by snow and ice. In Alaska, one storm in 1967–68 broke 28 percent of the stems in a 160-year-old black spruce stand *(46)*. Windthrow and breakage are two of the principal causes of mortality in black spruce stands in the Lake States; they must be considered when planning for harvesting black spruce stands.

Black spruce is easily killed by both ground and crown fires. It generally rates high in fire hazard, although many peatland stands have a low risk except during very dry periods *(26)*.

Black spruce growing in peatlands is especially susceptible to changes in the water table, which sometimes occur naturally as the result of damming of small streams by beavers, but also result from increased or impeded drainage caused by road construction.

Special Uses

The principal commercial use of black spruce both in Canada and the United States is for making high quality pulp with balanced strength properties. It is also used for lumber, Christmas trees, and other products. Black spruce Christmas trees were harvested in considerable numbers from natural stands until fairly recently, especially on poor sites in Minnesota *(26)*. Historically, black spruce has provided some highly specialized products, a few of which are still used occasionally: healing salves from spruce gum (exuded resin); beverages from twigs and needles; aromatic distillations from needles *(42)*; and binding material ("wattape")—from long, split roots—for birchbark canoes.

The spruce grouse depends mainly on black spruce stands for food and cover *(26)*. Birds with relatively high densities in black spruce stands during the summer include the ruby-crowned kinglet, magnolia warbler, Cape May warbler, and ovenbird. Birds such as the pine grosbeak, pine siskin, and crossbills commonly feed on black spruce seed.

Genetics

Genetic variation in black spruce is clinal, primarily along a north–south geographical gradient. Differences in photoperiod response, productivity, and survival rate have been shown to be related to the geographical area of seed origin. Although black spruce ecotypes related to upland and peatland sites have been reported from some areas, they have not been recognized in several studies of black spruce variation. Seed zones should be recognized, but separation of seed by peatland and upland location is probably not necessary *(30,31)*.

Hybrids between black spruce and red spruce are common, and introgressive hybridization between the two species has been reported in Nova Scotia, New Brunswick, and Quebec *(14,32)*.

A natural hybrid between black spruce and white spruce found in northern Minnesota has been called the Rosendahl spruce *(28)*. Intermediate forms between black and white spruce have been reported occasionally from other areas *(41)*, but the genetic isolation of these two species must be nearly complete.

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Picea pungens Engelm. **Blue Spruce**

Pinaceae **Pine family**

Gilbert H. Fechner

Blue spruce *(Picea pungens)* is also called Colorado blue spruce, Colorado spruce, silver spruce, and pino real. It is a slow-growing, long-lived tree of medium size that, because of its symmetry and color, is planted extensively as an ornamental. Because blue spruce is relatively scarce and the wood is brittle and often full of knots, it is not an important timber tree.

Habitat

Native Range

Blue spruce (fig. 1) is primarily native to the central and southern Rocky Mountains of the western United States. Its range extends from latitude 33° 50′ to 48° 54′ N. and from longitude 104° 45′ to 114° 00′ W.; the Rocky Mountain region in high mountains from southern and western Wyoming, eastern Idaho, south to Utah, northern and eastern Arizona, southern New Mexico, to central Colorado. It has been reported in isolated locations in north-central Montana *(83)*.

Climate

Blue spruce grows in a climatic zone that is generally cool and humid, with most of the annual precipitation occurring in the summer.

Mean annual temperatures where blue spruce is most commonly found in Colorado and the Southwest range from 3.9° to 6.1° C (39° to 43° F), with a January mean of –3.9° to –2.8° C (25° to 27° F) and a July mean of 13.9° to 15.0° C (57° to 59° F). Mean minimum January temperatures range from –11.1° to 8.9° C (12° to 16° F) and mean maximum July temperatures range from 21.1° to 22.2° C (70° to 72° F). The frost-free period from June to August is about 55 to 60 days *(5,69)*.

Average annual precipitation varies from 460 to 610 mm (18 to 24 in). Winter is usually precipitation-deficient, with less than 20 percent of the annual moisture falling from December through March. Fifty percent of the annual precipitation is rain that falls during the growing season *(5,69)*.

Although blue spruce grows best with abundant moisture, this species can withstand drought better than any other spruce *(36)*. It can also withstand extremely low temperatures (–40° C; –40° F), and it is more resistant to high insolation and frost damage than other associated species.

Soils and Topography

Basic information on soils and landforms needed for silvicultural decisions for blue spruce is limited. Both soils and landforms are very complex. Soils are young and vary widely in texture and physical and chemical properties according to the bedrock from which they originate. Glacial deposits, alluvium from streams, and material weathered in place from country rock are predominant, however *(2)*. The pH is 6.8 to 7.2, neutral to slightly alkaline *(21,62)*. The soils on which blue spruce grows naturally are in the order Mollisols and, to a lesser extent, in the orders Histosols and Inceptisols.

Blue spruce is found on gentle upland and subirrigated slopes, in well-watered tributary drainages, extending down intermittent streams, and on lower northerly slopes. Sites on which blue spruce grows are more moist than those of Rocky Mountain ponderosa pine *(Pinus ponderosa* var. *scopulorum)* and warmer than those of Engelmann spruce *(Picea engelmannii)* and subalpine fir *(Abies lasiocarpa) (2,65)*. In Utah, blue spruce is considered a pioneer tree species on wet soils *(21)* (fig. 2).

Blue spruce is characteristically found at elevations from 1830 to 2740 m (6,000 to 9,000 ft) in its northern range and from 2130 to 3050 m (7,000 to 10,000 ft) in its southern range *(27,65)*.

Associated Forest Cover

Blue spruce is a species of the montane zone in the central and southern Rocky Mountains, where it is the principal species of the Blue Spruce forest cover type (Society of American Foresters Type 216) *(27)*. Blue spruce is also named as a minor associate in four other types: Engelmann Spruce–Subalpine Fir (Type 206), Interior Douglas-Fir (Type 210), Cottonwood–Willow (Type 235), and Interior Ponderosa Pine (Type 237).

Over the bulk of its range, blue spruce is most frequently associated with Rocky Mountain Douglas-fir *(Pseudotsuga menziesii* var. *glauca)* and Rocky Mountain ponderosa pine and with white fir *(Abies concolor)* on mesic sites in the central Rocky Mountains. Blue spruce is seldom found in large numbers,

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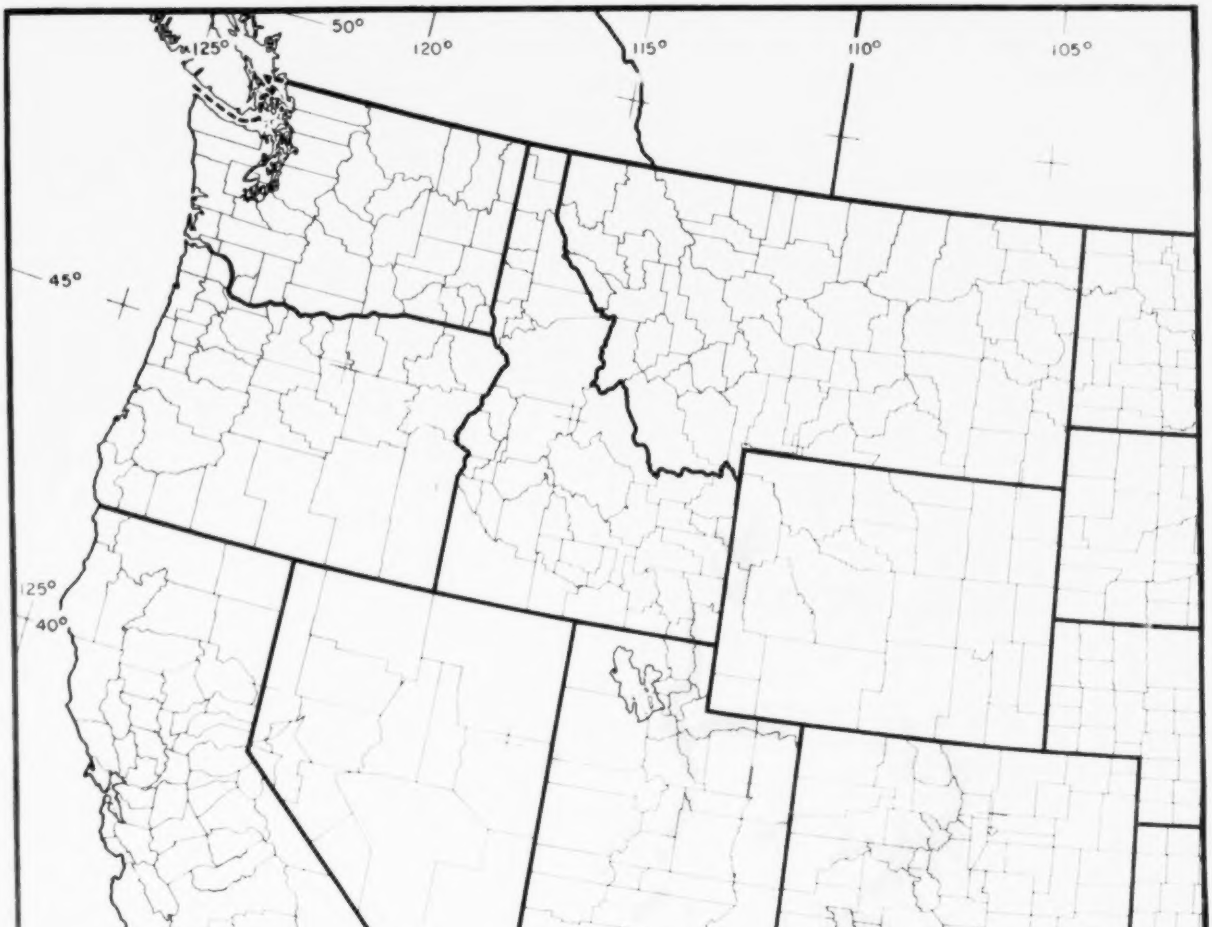
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Figure 1—*The native range of blue spruce.*

Figure 2—*Stand of blue spruce.*

but on streamside sites it is often the only coniferous species present.

Hardwoods associated with blue spruce are most commonly narrowleaf cottonwood *(Populus angustifolia)*, quaking aspen *(P. tremuloides)*, and occasionally balsam poplar *(P. balsamifera)*. Smaller streamside trees and common shrub associates are water birch *(Betula occidentalis)*, mountain alder *(Alnus tenuifolia)*, shrubby cinquefoil *(Potentilla fruticosa)*, common snowberry *(Symphoricarpos albus)*, chokecherry *(Prunus virginiana)*, and species of willow *(Salix)*.

On north-facing slopes, blue spruce, rarely found more than 9 to 12 m (30 to 40 ft) above the drainage bottoms, mixed with Douglas-fir or lodgepole pine *(Pinus contorta* var. *latifolia) (24)*. At higher elevations, above 2590 m (8,500 ft), blue spruce may mingle with Engelmann spruce, subalpine fir, and quaking aspen on moist sites, or lodgepole pine on drier sites *(49)*.

In its southern range (southwestern Colorado, Arizona, and New Mexico) blue spruce is part of the widespread mixed conifer forest as a component of several diverse habitat types constituting topoedaphic climaxes in stream bottoms and meadow borders. In general, blue spruce dominates habitats that are too warm for Engelmann spruce and subalpine fir and that are wetter than those typically occupied by ponderosa pine. Shrub associates include Rocky Mountain maple *(Acer glabrum)*, western serviceberry *(Amelanchier alnifolia)*, common juniper *(Juniperus communis)*, and Gambel oak *(Quercus gambelii)*, as well as alders and willows on the moister sites *(50,65)*.

In its northern range (northern Wyoming, Idaho, and Montana), blue spruce is found only in scattered locations under established stands of narrowleaf cottonwood and among scattered ponderosa pine, with Engelmann spruce and white spruce *(Picea glauca)* associated with the species in the extreme north *(64,84)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Blue spruce is monoecious. Male strobili develop throughout the living crown of the tree, although they are usually more frequent in the upper one-half of the crown. They commonly develop in whorls of three to five at the base of the current vegetative growth, or singly in subterminal positions *(25)*. Female strobili develop in the upper 10 to 25 percent of the live crown of mature trees. They usually occupy terminal positions on lateral branchlets.

Most male strobili of blue spruce are rose red when they emerge from the buds, but on occasional trees they appear yellowish-green[1]. A single male strobilus, containing 100 sporophylls, may produce about 370,000 pollen grains. The female strobili consist of 175 to 225 scales and thus have a potential to produce 350 to 450 seeds per cone. Pollen is shed in May or June, depending upon altitude.

For a short period of time following emergence from the bud, the scales of the female strobili are a pale greenish color. As peak receptivity is reached, however, the scales of the strobili on most trees become red and are reflexed 90 degrees or more toward the base of the strobilus, which assumes an erect position on the twig. Occasional trees produce yellowish-green strobili[1]. Approximately 2 weeks following initial receptivity, the female strobilus moves from this erect position to about 45 degrees above horizontal. In another week, 50 percent of the cones on a tree are 45 degrees below horizontal to pendent. During the fourth week, all cones become pendent and reach their full size *(24,26,28)*.

Seed Production and Dissemination—Blue spruce is generally considered to be from good to prolific in seed production, yielding full crops of cones every 2 or 3 years *(77,84)*. Some intermediate years are complete failures *(24)*. Seed production begins at approximately 20 years, and optimum seed-bearing age is reached between 50 and 150 years *(88)*. Cones mature in August of the first year; seed shed begins

[1] Male and female strobili on a given tree are the same color, whether red or green

from early to late September, depending on altitude, and continues into the winter *(26,77)*. The seed is wind disseminated, seedfall diminishing rapidly as distance from the source increases; most seeds fall within 90 m (300 ft) of the upwind timber edge *(2)*.

It is unlikely that heavy cone crops will occur in successive years on a single blue spruce tree, because the female strobili occupy terminal positions on lateral branchlets. Such terminal positions are at a minimum in the year following one of high seed production, because once a strobilus is differentiated from an apical meristem, only the strobilus develops at that position during the following growing season. If a whorl of new axillary buds is produced on the branchlet at the base of the developing cone, these buds ordinarily produce vegetative shoots for one season before female stobili are again differentiated. Thus, although blue spruce cones occasionally occupy sessile, axillary positions, the likelihood of heavy seed crops occurring more frequently than every 2 years is very remote *(24)*.

Seedling Development—Seeds of blue spruce germinate on a variety of media, although natural reproduction is mostly confined to exposed mineral soil with side shade and overhead light in the vicinity of seeding trees. Natural reproduction is scanty, probably because the lightweight seed is prevented from coming into contact with mineral soil by the dense herbage, grass, or other ground-cover vegetation that is usually abundant in the habitat of the species *(84)*.

Seeds of blue spruce were once thought to show embryo dormancy. It is now known, however, that blue spruce seeds germinate promptly and completely without prior stratification, under a wide range of temperatures, with or without light *(46)*. Germination is epigeal *(77)*.

In most parts of the blue spruce range natural germination of seed takes place in the spring or summer following dispersal and is dependent on adequate precipitation *(51)*.

Spring and early summer drought periods occur regularly in the Southwest. Although soils of the mixed conifer forest are wet at the end of winter from melting snows, these drought periods during the growing season create soil moisture deficits that are critical to initial seedling survival. Fall moisture deficits common over the remainder of the range are less limiting to seedling establishment and usually do not kill seedlings established for 2 years or more except on severely affected sites *(2,52)*.

Blue spruce seedlings are more sensitive to day temperatures between 13° and 31° C (55° and 88° F) than to night temperatures between 7° and 25° C (45° and 77° F) *(86)*.

Under greenhouse conditions, blue spruce seedlings are affected by supplemental light. They grow continuously when exposed to photoperiods exceeding 16 hours and enter dormany within 4 weeks under photoperiods of 12 hours or less. Dormancy is prevented under 12-hour photoperiods by 2-hour light breaks of red light (1.70 µw/cm^2 @ 650 nm) or high intensity white light (2,164.29 µw/cm^2 @ 400 to 800 nm) given in the middle of the 12-hour night *(94)*, or by one-minute light breaks every 30 minutes throughout the night *(85)*.

The establishment of blue spruce seedlings under natural conditions is probably benefited by moisture availability and shading, which prolong snow and soil moisture in late spring.

Early growth of blue spruce seedlings is very slow. In a Michigan nursery study, the tallest of 50 populations averaged 15.7 cm (6.2 in) at 2 years *(40)*. In North Dakota, the tallest of seven sources was 58.4 cm (23.0 in), 5 years after outplanting *(18)*. Similarly, in a plantation in the southern range, trees were 48.5 to 59.2 cm (19.1 to 23.3 in) tall after five growing seasons *(53)*.

Vegetative Reproduction—Natural vegetative reproduction of blue spruce has not been reported. The species does not sprout from the stump or root, but the development of epicormic branches on the trunk is common. Grafting and air-layering have been practiced successfully for many years to perpetuate desired horticultural varieties *(32,60,63, 74,91)*. Success has also been achieved through the rooting of hardwood or greenwood stem cuttings, especially in sand-peat-soil media, or hydroponically *(56,79,81,93)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Blue spruce is apparently a long-lived tree, surviving up to 600 years or more. Diameter growth is slow; trees 10 to 13 cm (4 to 5 in) in d.b.h. may be 125 to 135 years old; at 46 to 56 cm (18 to 22 in), they may be 275 to 350 years of age *(84)*. The "1982 National Register of Big Trees" lists the largest blue spruce as 154.4 cm (60.8 in) in d.b.h. and 38.4 m (126 ft) tall, on the Gunnison National Forest, CO.

Few growth and yield data are available for blue spruce. In one study, in a mixed conifer forest in east-central Arizona, blue spruce was found to constitute a total of 0.7 m^2/ha basal area (3.05 ft^2/acre) of a total of 40.8 m^2 (177.7 ft^2). The 728-ha (1,800-acre) forest consisted of Douglas-fir (31.4 percent), quaking aspen (15.9 percent), white fir (14.5 percent), ponderosa pine (14.1 percent), Engelmann spruce (13.5 percent), southwestern white pine (*Pinus strobiformis*) (5.6 percent), corkbark fir (*Abies lasiocarpa* var. *arizonica*) (3.3 percent), and blue spruce (1.7 percent). In this study the annual basal area growth for blue spruce was found to be 2.9 percent, greater than that of any other species except corkbark fir, which was 3.7 percent per year *(22)*. The total basal area growth for blue spruce, 0.008 m^2 (0.088 ft^2) per year, was distributed as shown in table 1.

Rooting Habit—Young seedlings of blue spruce are shallow rooted, with roots penetrating the soil only about 6.4 cm (2.5 in) during the first year *(50)*. Although blue spruce tissue is not damaged much by freezing, seedling losses can result from frost heaving. Shade in late spring and early fall minimizes such frost-heaving losses *(2,69)*.

Even in mature trees, the root system of blue spruce is relatively shallow, compared to that of Douglas-fir and ponderosa pine, adapting it to the moist site on which it usually grows. In spite of the shallow root system, blue spruce is decidedly windfirm *(36)*.

Pruning roots of blue spruce 5 years before transplanting doubles the total root surface area of 2-meter-tall trees at transplanting time. It also increases the concentration of the root system within the dripline from 40 to 60 percent, an advantage in landscape plantings *(90)*.

Reaction to Competition—Blue spruce is classed as intermediate in tolerance of shade, the middle of five tolerance categories for western conifers. It is less tolerant than subalpine fir, Engelmann spruce, and white fir; it is similiar in tolerance to, or slightly more tolerant than Douglas-fir; it is more tolerant than southwestern white pine, ponderosa pine, lodgepole pine, Rocky Mountain juniper, quaking aspen, or its other moist-site hardwood associates *(4,27,52,62)*.

On cool sites, a dense or moderately dense canopy favors regeneration of subalpine fir, blue spruce, white fir, and Engelmann spruce, to the exclusion of Douglas-fir. On warm sites, an open canopy favors ponderosa pine, whereas a moderate canopy favors Douglas-fir *(92)*.

Blue spruce occurs in various seral stages, from pioneer to climax, in 32 currently recognized habitat types *(28)*. The exact successional status depends on the location within its geographic range and on its immediate associates. For example, in the Southwest, blue spruce represents a topo-edaphic climax, one in which environmental factors compensate for one another *(17)*; here it reproduces and is present in all sizes, along stream banks, in well-watered tributaries, on gentle lower slopes, and in forest borders of grassy meadows. On these sites, ponderosa pine and Douglas-fir may be long-lived seral species, white fir and southwestern white pine may occur as minor seral species, and subalpine fir may be of accidental occurrence *(58,65)*. Blue spruce may also form climax stands with Engelmann spruce on slopes and in drainages at higher elevations and with Douglas-fir and white fir *(1)* on lower slopes and north aspects at lower elevations *(65)*. Blue spruce may be a minor seral species in white fir- and subalpine fir-dominated forests on cooler sites *(58)*, and it may constitute a pioneer species on wet sites *(21)*.

In Utah, blue spruce is a climax species in three distinct environments: gentle to steep mountain slopes, floodplains and valley bottoms at lower elevations, and montane sites on alluvium or aqueaceous north-aspect deposits *(23)*. Almost exclusively, sites that support climax stands of blue spruce have parent materials of limestone or calcareous sandstone. Thus, blue spruce probably constitutes an edaphic climax on these sites *(62,71)*. On Utah sites, quaking aspen is the prinicipal seral species, except in the Uinta Mountains, where the seral role is assumed by lodgepole pine. At the higher altitudes in Utah, blue spruce becomes a minor seral species to subalpine fir *(71)*.

Damaging Agents—Several insects are known to attack developing cones and seeds of blue spruce, but

Table 1—Annual basal area growth for blue spruce in east-central Arizona (22).

D.b.h. class	Percent of stand	Incremental growth	
		m^2/ha	$ft^2/acre$
0.3 to 17.5 cm 0.1 to 6.9 in	49	0.004	0.017
17.8 to 27.7 cm 7.0 to 10.9 in	18	0.001	0.006
27.9 to 42.9 cm 11.0 to 16.9 in	18	0.001	0.006
43.2 to 58.2 cm 17.0 to 22.9 in	10	0.001	0.004
58.4 cm and larger 23.0 in and larger	5	—	0.002
Total	100	0.007	0.035

damage caused by insects is not heavy *(55)*. The spruce seed chalcid *(Megastigmus piceae)* is found throughout the range of the host. Larvae of the spruce seed moth *(Laspeyresia youngana)* and the cone cochylid *(Henricus fuscodorsana)* bore through cone scales near the axis of the cones, destroying both scales and up to 10 percent of the seeds. Larvae of the spruce coneworm *(Dioryctria reniculelloides)* mine young cones in addition to feeding on tender terminal growth and its foliage *(34,45,54)*.

In addition to those attacking developing cones and seeds, other insects occasionally damage blue spruce *(34)*. The larvae of the western spruce budworm *(Choristoneura occidentalis)* feed on old needles in late April, then mine developing buds and defoliate new tree growth *(59)*. Heavy, repeated attacks kill the tree.

Less serious damage can be caused by the spruce needle miner *(Taniva abolineana)*, and another needle miner, *Coleotechnites piceaella (34,43,54)*. The Cooley spruce gall aphid *(Adelges cooleyi)* and the pine leaf aphids *(Pineus pinifoliae* and *Pineus similis)* cause the formation of cone-shaped galls. The former may be of consequence on seedlings and saplings.

Other insects that attack blue spruce are the green spruce aphid, *Cinara fornacula*, and the related *Cinara coloradensis*, which feed on terminal twigs, as does the white pine weevil *(Pissodes strobi)*. Twig beetles, *Pityophthorus* spp., may attack injured trees. *Dendroctonus rufipennis*, the spruce beetle, is also found on blue spruce. *Ips pilifrons*, an engraver beetle which attacks recently downed trees, may deprive the spruce beetle of favorable breeding places, thereby reducing the threat of a spruce beetle outbreak *(34,72)*. Secondary insects are *Dryocoetes affaber* and the four-eyed spruce beetle *(Polygraphus rufipennis)*. Ambrosia beetles, *Gnathotrichus sulcatus*, and *Trypodendron bivattatum*, and the golden buprestid *(Buprestis aurulenta)*, a flatheaded borer, attack the wood.

The rust *Chrysomyxa pirolata* infects the cones of blue spruce. Seed production is not greatly affected by this disease, however, although malformation of the cones may interfere with seed dispersal *(67)*. Seed viability in rust-infected cones may be reduced, but seeds are not totally destroyed.

A variety of diseases also attack seedlings, leaves, stems, and roots of blue spruce. Damping-off, caused by *Phytophthora cinnamomi*, kills new seedlings, as does the cylindrocladium root rot, caused by *Cylindrocladium scoparium (11,48)*. Nematodes may reduce root growth of seedlings in nurseries *(30,37)*. Low seedling vigor is also caused by the root lesion nematode, *Pratylenchus penetrans (48)*, and snow molds may cause nursery losses during seasons of heavy snow *(82)*.

Leucocytospora kunzei (Syn.: *Cytospora kunzei*) is widespread in northeastern United States and may cause cankers on one-fourth to one-half of the branches of blue spruce. Although usually not fatal, branch loss dramatically reduces the aesthetic value of landscape trees *(35,73)*. *Phomopsis occulta* causes a tip blight on blue spruce; it is characterized by downward curling and necrosis of expanding shoots, where stem cankers and sap exudate commonly occur *(78)*. Western spruce dwarf mistletoe *(Arceuthobium microcarpum)* causes mortality in infected stands two to five times greater than in healthy stands, and heavily infected trees may show a 10-year volume loss of up to 40 percent *(61)*.

Three species of *Chrysomyxa* cause needle rusts and moderate amounts of shedding of new needles on blue spruce. Another needle cast fungus, *Rhizosphaera kalkhoffii*, damages Christmas tree plantations of blue spruce in the Midwest and the East. Serious damage is not associated with natural stands of this species although the disease was first reported on blue spruce in its native range in Arizona *(44,68,89)*. *Chrysomyxa arctostaphyli* causes the perennial yellow witches' broom on blue spruce branches; *Arctostaphylos uva-ursi*, the common kinnikinnik, serves as host of stage 3 of the fungus *(70)*. *Armillaria mellea* and *Inonotus tomentosus* both cause root rot, and *Phellinus pini*, *Fomitopsis pinicola*, *Climacocystis borealis*, and *Polyporus caesius* are common heart rots *(48)*.

Special Uses

Blue spruce is valued mainly for its appearance. Shortly after the species was discovered in 1861, writers described it as "a finely shaped tree" and "the most beautiful species of conifer," alluding to the symmetrical, pyramidal form and the glaucous, bluish or silvery-gray foliage that some trees of the species display. The needle coloration, caused by the presence of surface waxes *(76)*, apparently intensifies with tree age *(13,14)*. These traits of symmetry and blue or silver-gray cast, so common in horticultural plantings, are only occasionally found in natural stands. In nature, trees with similar color tend to occur in small, local populations, suggesting genetic control of the color trait.

Blue spruce is widely used as an ornamental, not only in the United States, but in Europe, where it was introduced late in the 19th century. At least 38 cultivars of blue spruce have been named, based primarily on leaf coloration and crown form *(3,19)* (table 2). Although young blue spruce usually show a pronounced layering of stiff branches, which give it a distinct pyramidal form, the branches begin to droop and the crown becomes thin and irregular as the tree ages. The trunk tapers rapidly, and epicormic shoots commonly develop, giving the tree a ragged appearance. Blue spruce is prized as a Christmas tree, and plantations have been established in its native range and in northcentral and northeastern United States.

Genetics

Population Differences

In a study of seven blue spruce provenances from Arizona, Colorado, Utah, and Wyoming, grown in North Dakota, 5-year survival varied from 22 percent for the Targee National Forest, WY, source to 96 percent for an Ashley National Forest, UT, source *(18)*. In the same study, height differed significantly among the sources; the two sources from Ashley National Forest represented the tallest (57.3 cm; 22.6 in) and the shortest (37.5 cm; 14.8 in). No latitudinal or altitudinal pattern of survival, growth, or frost resistance seemed apparent.

In a Michigan nursery study of progenies from 50 populations collected throughout its range, 2-year-old blue spruce seedlings from Colorado, New Mexico, and Arizona grew more rapidly than those from Utah, Wyoming, or Montana. The average heights of the 10 tallest populations ranged from 18.8 to 16.1 cm (7.4 to 6.3 in) *(40)*.

Variation in foliage color is apparently under strong genetic control *(15)*, although the mechanism of inheritance is not presently known. Because there is no consistency in blue color from any one source, color variation is a characteristic to expect with seed-produced trees *(47)*. Two-year-old progenies from Arizona and New Mexico seed sources show a much higher incidence of "blueness" than those from other areas *(40)*. However, little or no difference has been detected between seedlings with glaucous (bluish) or non-glaucous (greenish) needles in photosynthetic rate, transpiration rate, and moisture retention *(75)*. These studies suggest that genetic variation in natural populations of blue spruce does not conform to a clinal pattern. Rather, the pattern appears to be ecotypic, with considerable stand-to-stand variation and individual tree variation.

Significant variation exists among populations in the concentration of terpenes derived from cortical tissue. Five populations, each consisting of 10 selected seed trees, differed significantly in the concentration of each of eight monoterpenes in a Michigan study. Although the total percentages of the eight monoterpenes were similar among the populations, the Utah, Colorado, and Wyoming populations were distinct from the New Mexico and Arizona populations due to percentages of specific monoterpenes. For example, the average percentage of α-pinene was 14.3 for the three northern populations and 8.5 for the two southern ones, whereas β-phellandrene averaged 0.58 percent for the northern populations and 0.89 percent for the southern populations *(39)*.

Table 2—Some cultivated varieties of blue spruce.

Cultivar	Characteristics
'**Argentea**' Rosenthal	Silvery white
'**Aurea**' Niemitz	Golden yellow
'**Bakeri**' Bailey	Deep bluish white, long-leaved
'**Caerulea**' Beissner	Bluish white
'**Compacta**' Rehder	Dwarf, compact, densely flat-topped
'**Glauca**' Beissner	Bluish green; collective name for all glaucous-leaved cultivars
'**Glauca Pendula**' Koster ex Beissner	Pendulous, bluish leaves, strongly sickle-shaped
'**Hoopsii**' Hoops ex F. J. Grootend.	Dense, pyramidal; leaves very silvery
'**Hunnewelliana**' Hornibr.	Dwarf, dense, pyramidal; leaves pale green
'**Koster**' Boom	Pyramidal, pendulous-branched, with main branches almost horizontal; leaves bluish white to silvery white
'**Moerheimi**' Ruys	Pyramidal, slender, dense, compact; leaves deep blue
'**Thomsen**' Thomsen	Pyramidal; leaves whitish to silvery blue, long
'**Viridis**' Regel	Dull green

Large differences in monoterpene yield exist in xylem, bark, and needles of individual blue spruce trees, and variation in terpene yield among trees is significant. The concentration of the terpenes in the needles and xylem varies with crown position, the yield increasing with tree height in the xylem and decreasing with tree height in the needles. These yields are correlated with the proportions of resin canals in the respective tissues *(66)*.

Several investigators have reported different results in blue spruce seedlings grown under accelerated greenhouse conditions *(20,39,40,41)*. In a recent study, height growth of 75 single-tree Colorado sources, grown under accelerated greenhouse conditions, varied significantly among six seed zones but not among families within a seed zone. Seed zone averages ranged from 22.2 cm for the tallest to 14.2 cm for the shortest during the 140-day test period *(20)*.

In their reports of a rangewide provenance study of blue spruce conducted in Michigan, investigators noted that the southern sources of blue spruce did not grow as well under accelerated greenhouse conditions as did the northern sources *(6,8,41)*. In contrast, in the Colorado study, southern Colorado sources generally outgrew the northern Colorado sources.

It is interesting to note that in field plantations subsequently established in several midwestern states and Quebec with their blue spruce sources, the Michigan investigators observed a reversal of the variation patterns that they had observed in the greenhouse. In the field plantations, the southern sources outgrew the northern sources *(9,10,87)*. Thus, growth of the seedlings studied in Colorado in the greenhouse followed much the same patterns as the seedlings that were grown outdoors in the Michigan studies.

In only a single study has the date of bud set been recorded in blue spruce. Within latitudinal groups in Colorado, bud set varied with elevation of the seedling seed source, the high-elevation sources setting bud much sooner than the low-elevation sources *(20)*. Some investigators *(6,87)* have found no consistent pattern or date of bud break in the 400 widely distributed sources of blue spruce studied. And others *(10)* found that bud break was variously related to longitude but not to elevation. Yet the results of the Colorado study, based on relatively intensive elevational sampling, show a relationship between latitude and elevation of seed origin and the date of bud set.

Thus, whereas research results support the notion that natural variation of most parameters that have been studied in blue spruce conforms to a discontinuous pattern geographically *(18,20,39,40,87)*, variation in date of bud set conforms to a local altitudinal clinal pattern *(20)*.

Hybrids

From studies of morphological features of blue spruce and Engelmann spruce, it has been concluded that these two species do not hybridize in nature, although no morphological character absolutely separates the two *(16)*. Considerable overlap in cone size has been found; Engelmann spruce cones vary from 2.8 to 5.8 cm (1.1 to 2.3 in) and blue spruce cones vary from 4.5 to 10.7 cm (1.8 to 4.2 in) in neighboring populations measured in northern Colorado *(33)*. Cone and seed characteristics are often found to be indistinguishable *(40)*.

Controlled crosses between blue spruce and Engelmann spruce obtained up to 2 percent sound seed set when Engelmann spruce was the female parent *(29)*. The reciprocal cross was also successful. Only occasional embryos developed following crosses between the two species, but, more frequently, reproductive failure occurred prior to embryo formation *(57)*.

Much overlap between blue spruce and Engelmann spruce in cortical monoterpene content has also been observed, although species differences in the quantity of several of the compounds are statistically significant. Oleoresins of blue spruce contain higher levels of tricyclene, α-pinene, camphene, and bornyl acetate, whereas Engelmann spruce oleoresins contain higher levels of β-pinene, 3-carene, terpinolene, and several unknown compounds *(80)*.

These and other results *(42)* indicate that hybridization between blue spruce and Engelmann spruce is possible. This might account for the various intergrades between blue spruce, white spruce, and Engelmann spruce that have been reported in Montana *(83)*.

Information on inheritance patterns for certain characteristics of blue spruce, although somewhat inconclusive, is provided by results of half-sib and full-sib progeny studies involving that species. For example, in a Canadian study *(13,14)*, inheritance of needle coloration was investigated using such controlled crosses. A qualitative rating scale of one (green) to four (silvery blue) was used for comparison. Although the proportion of blue seedlings was not significantly related to the blue color ratings of their open-pollinated parents, the needle-color ratings of 10-year progeny were related to those of their self-pollinated parents (r = 0.83). One selfed tree produced 94 percent blue progeny.

As is true for certain other coniferous species, albinism in blue spruce is apparently controlled by a single gene. The proportion of normal (green) to albino seedlings derived from self-pollinated seeds of two different trees produce a good fit to a 3:1 ratio, suggesting heterozygosity for a simple lethal factor *(12)*.

In Michigan studies, hybrid progeny from crosses between white spruce and blue spruce showed a slight, but nonsignificant, increase in germination rate over the parental half-sib progeny, and at 42 weeks, needle length was intermediate between those of the parental progeny. Although the hybrid progeny as a group displayed intermediacy in 3-carene biosynthesis ability between the two parents, individual-tree values showed genetic segregation in the open-pollinated (half-sib) blue spruce progeny and uniformity in the open-pollinated (half-sib) white spruce progeny *(42)*. Yet, the range of values for 3-carene biosynthesis ability is controlled by a single pair of alleles, as had been shown for western white

Table 3—Summary of inheritance of various traits from crosses among red, white, and blue spruces. Adapted from Bongarten and Hanover, 1982 *(7)*.

Spruce combination	Character response
(White x blue) x white (backcross)	– Similar to white spruce in all measured characters.
(White x blue) x blue (backcross)	– Similar to blue in 6-month, height, needle curvature, and 3-carene concentration. – Similar to white in needle serrations. – Intermediate in β-pinene concentration.
(White x blue) x red (trihybrid)	– Similar to red in needle serrations, limonene concentration, and needle curvature. – Similar to white x red in needle color. – Similar to white x blue in 3-carene and β-pinene concentrations.

pine *(Pinus monticola)* *(38)*. However, when natural populations of blue spruce were studied for this characteristic, allele frequencies for the 3-carene gene did not conform to expected values in Colorado and New Mexico populations, although they did conform to expected single-gene frequencies in the Utah, Arizona, and Wyoming populations *(39)*. These apparent discrepancies could be artifacts of sample size or other unknown factors.

Whereas the initiation date of germination of hybrid seed has been found to be intermediate between parental (half-sib) seed of blue spruce and Engelmann spruce, cotyledon number, mean day of total germination, and hypocotyl color tend to be similar to those of female parent *(29)*. That cotyledon number is under strong maternal control, as it also is in white spruce *(31)*, is supported by a recent study, in which cotyledon number differed significantly (P = .001) between half-sib Colorado families but not within those families *(20)*.

From studies of controlled crosses among white spruce, blue spruce, and red spruce *(Picea rubens)*, F_2 progeny of white spruce × blue spruce crosses were found to be much stunted in height and in needle length *(7)*. Further results of findings among these species are summarized in table 3.

In summary, it would appear that for most needle, chemical synthesis, and germination characteristics that have been studied in blue spruce, the gene action is quantitative. Exceptions to this seem manifest in the biosynthetic ability of 3-carene and in the production of albino seedlings, which may be single-gene controlled, and cotyledon number, hypocotyl color, and mean germination date, which may be under strong maternal influence in that species.

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Picea rubens Sarg. Red Spruce

Pinaceae Pine family

Barton M. Blum

Red spruce (*Picea rubens*), also known as yellow spruce, West Virginia spruce, eastern spruce, and he-balsam, is one of the more important conifers in the northeastern United States and adjacent Canada. It

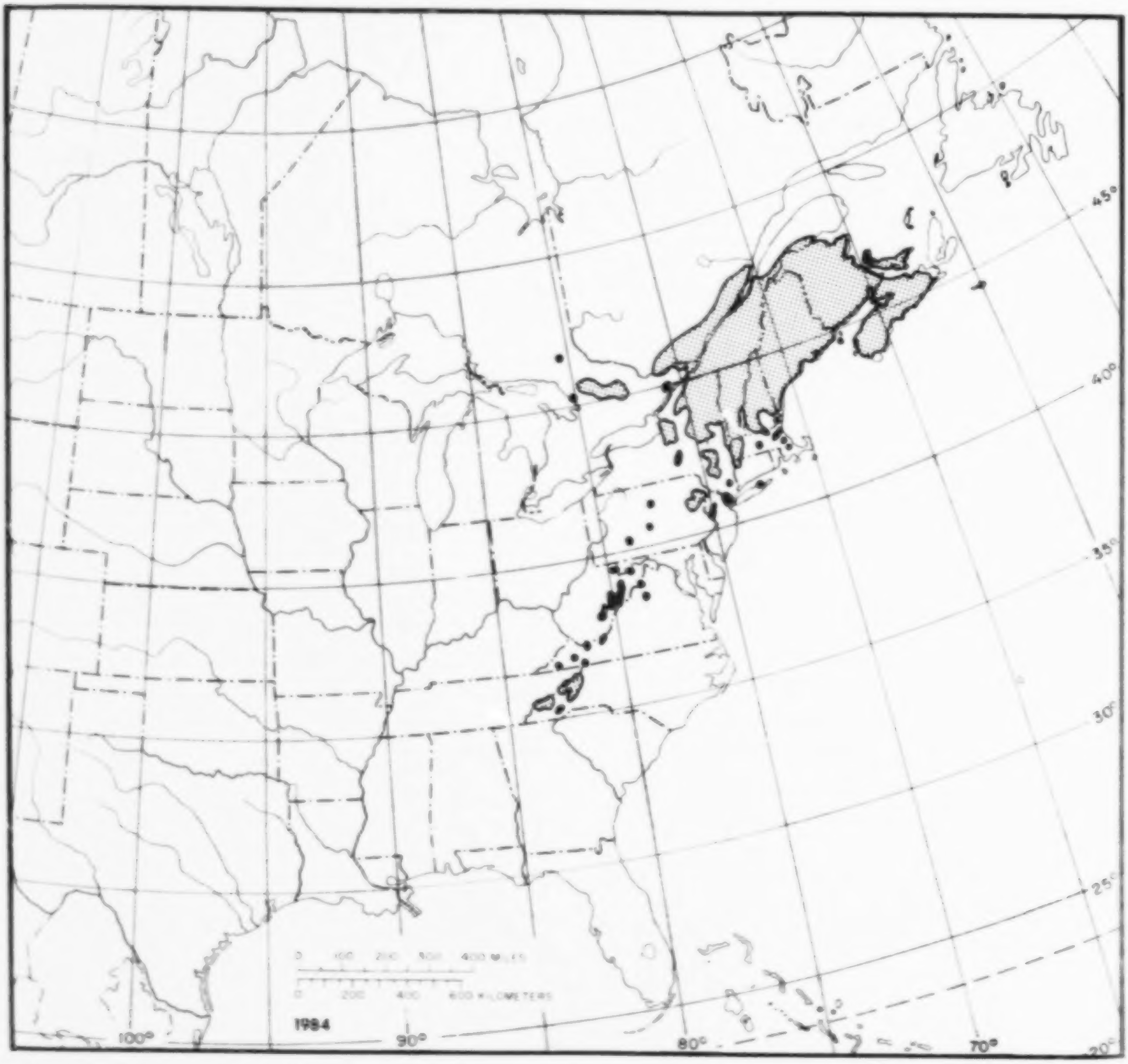
45°
40°
35°
30°
25°
20°
100°
90°
80°
70°
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
1984

Figure 1—*The native range of red spruce.*

The author is Research Forester, Northeastern Forest Experiment Station, Radnor, PA.

is a medium-size tree that may grow to be more than 400 years old. The wood of red spruce is light in color and weight, straight grained, and resilient. It is used for making paper, for construction lumber, and for musical stringed instruments. Its many uses rival those of eastern white pine *(Pinus strobus) (21)*.

Habitat

Native Range

The range of red spruce (fig. 1) extends from the Maritime Provinces of Canada west to Maine, southern Quebec, and southeastern Ontario, and south into central New York, eastern Pennsylvania, northern New Jersey, and Massachusetts. It also grows south along the Appalachian Mountains in extreme western Maryland, and eastern West Virginia, and north and west in Virginia, western North Carolina, and eastern Tennessee. Discontinuous stands may also be found in Haliburton Township, in Algonquin Provincial Park, and near Sturgeon Falls in Nippising Township, and in the southwestern Parry Sound District in Ontario, Canada.

Climate

Red spruce grows best in a cool, moist climate. The climate of the northeastern part of its range can be summarized as follows: annual precipitation (total), 910 to 1320 mm (36 to 52 in); annual snowfall, 203 to 406 cm (80 to 160 in); days with snow cover, 100 to 140; January temperature, -7° to -1° C (20° to 30° F) maximum and -18° to -13° C (0° to 8° F) minimum; July temperature, 21° to 27° C (70° to 80° F) maximum, and 11° to 14° C (52° to 58° F) minimum; frost-free days, 90 to 150 *(28)*. Red spruce attains maximum development in the higher parts of the southern Appalachian Mountains where the atmosphere is more humid and the rainfall heavier during the growing season than in other parts of its range *(47)*. Local extension of the range of red spruce, as along the southern Maine coast, is related to marine exposure, which provides a cool growing season and ample moisture supply *(8)*.

Soils and Topography

The soils where red spruce and its associates grow are mostly acid Spodosols, Inceptisols, and sometimes Histosols with a thick mor humus and a well-defined A_2 horizon—characteristics commonly associated with abundant rainfall, cool climates, and softwood cover *(11)*. Commonly, the pH of these soils ranges from 4.0 to 5.5. In northern New England, red spruce is found predominantly on shallow till soils that average about 46 cm (18 in) to a compact layer. It will grow on many sites unfavorable for other species, such as organic soils overlying rocks in mountainous locations, steep rocky slopes, thin soils, and wet bottomland *(26)*. On poorly drained soils, lack of aeration limits growth *(22)*.

In the northern part of its range, red spruce (fig. 2) grows at elevations from near sea level to about 1370 m (4,500 ft) *(22)*. In the southern Appalachian Mountains it comes in at elevations as low as 1370 m (4,500 ft) and from there to about 1520 m (5,000 ft) it is mixed with hardwoods and eastern hemlock *(Tsuga canadensis)*. At 1520 m (5,000 ft) balsam fir *(Abies balsamea)* joins with red spruce to form the dominant spruce-fir climax type. In West Virginia, spruce-fir stands are found as low as 980 m (3,200

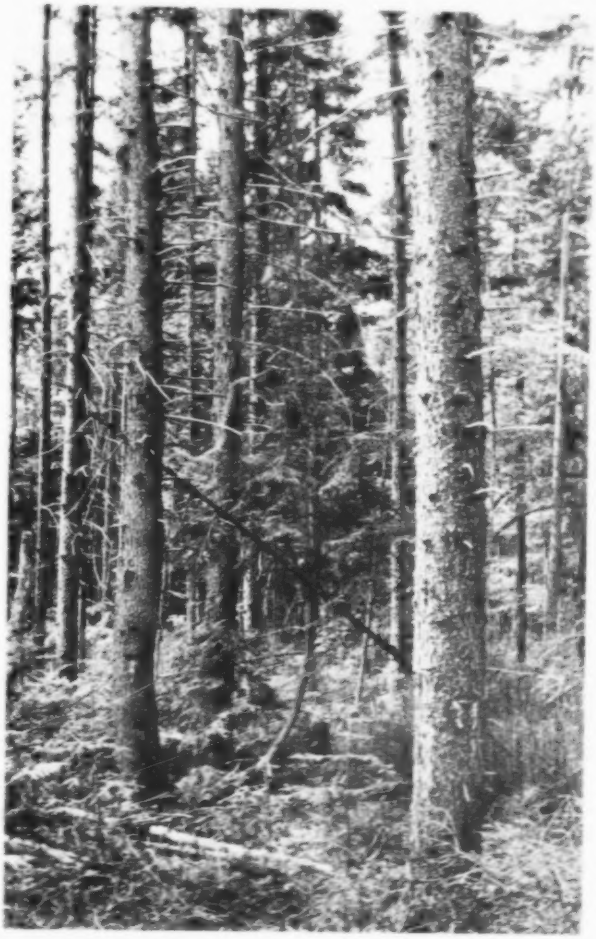

Figure 2—*A red spruce stand.*

ft). Above 1890 m (6,200 ft) in the southern Appalachians, red spruce appears less frequently than Fraser fir *(Abies fraseri) (47)*. In the White Mountains of New Hampshire, balsam fir is the predominant species above 1220 m (4,000 ft) but red spruce is well represented from about 790 to 1010 m (2,600 to 3,300 ft) *(27)*.

Associated Forest Cover

Pure stands of red spruce comprise the forest cover type Red Spruce (Society of American Foresters Type 32). Red spruce is also a major component in 5 and a minor component in 13 other forest cover types *(10)*:

5	Balsam Fir
12	Black Spruce
16	Aspen
17	Pin Cherry
18	Paper Birch
21	Eastern White Pine
22	White Pine–Hemlock
23	Eastern Hemlock
25	Sugar Maple–Beech–Yellow Birch
30	Red Spruce–Yellow Birch
31	Red Spruce–Sugar Maple–Beech
33	Red Spruce–Balsam Fir
34	Red Spruce–Fraser Fir
35	Paper Birch–Red Spruce–Balsam Fir
37	Northern White-Cedar
60	Beech–Sugar Maple
107	White Spruce
108	Red Maple

Some of the shrubs associated with red spruce are: blueberry *(Vaccinium* spp.), hobblebush *(Viburnum lantanoides)*, witherod *(V. cassinoides)*, rhodora *(Rhododendron canadense)*, lambkill *(Kalmia angustifolia)*, mountain-holly *(Nemopanthus mucronata)*, speckled alder *(Alnus rugosa)*, red raspberry *(Rubus idaeus* var. *strigosus)*, creeping snowberry *(Gaultheria hispidula)*, wintergreen *(G. procumbens)*, fly honeysuckle *(Lonicera canadensis)*, gooseberry *(Ribes* spp.), witch-hazel *(Hamamelis virginiana)*, downey serviceberry *(Amelanchier arborea)*, beaked hazel *(Corylus cornuta)*, and Canada yew *(Taxus canadensis)*.

A number of mosses and herbs are also found growing in red spruce forest types. Certain mosses, herbs, and shrubs, however, have been shown to be related to site quality of red spruce *(22)*. The three main associations, *Hylocomium/Oxalis*, *Oxalis/Cornus*, and *Viburnum/Oxalis*, in that order, indicate increasing site productivity and increasing hardwood competition. Similar site types in the higher elevations of the Appalachian Mountains of North Carolina include *Hylocomium/Oxalis* on north-facing slopes above 1520 m (5,000 ft), *Oxalis/Dryopteris* at high elevations and all exposures, and the best site type for red spruce and Fraser fir, *Viburnum/Vaccinium/Dryopteris (47)*.

The *Oxalis/Cornus* association is considered the best for growing conditions in the northern part of the range. On these sites the soil is rich enough for red spruce but not fertile enough for the tolerant hardwoods to offer serious competition *(22)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red spruce is monoecious; male and female flower buds open in May in axils of the previous year's shoots on different branches of the same tree. The pendant male flowers are bright red; female flowers are erect and bright green tinged with purple *(21)*. Although cone buds differentiate as early as July preceding flowering in the following spring, they are difficult to distinguish until September. For experienced workers they provide a possible means of identifying seed years at that time. The cones mature from about mid-September to early October, the autumn following flowering *(41)*. Cones are 3 to 4 cm (1.3 to 1.5 in) long, light reddish brown, with rigid, rounded scales often slightly toothed on the edges. Cones are receptive to pollen when fully open, a condition which lasts for only a few days.

Seed Production and Dissemination—Good seed crops occur every 3 to 8 years, with light crops during intervening years *(22)*. Red spruce cones number about 140/liter (5,000/bu), which yields 454 to 680 g (1.0 to 1.5 lb) of seeds. The number of cleaned seeds per kilogram ranges between 220,000 and 637,000 (100,000 and 289,000/lb), with an average of about 306,000 (139,000/lb) *(41)*.

Red spruce seeds fall about 1.2 m (4 ft) per second in still air; the following formula determines distance of travel for wind-disseminated spruce seeds at various heights *(47)*:

$$D = S^h\ (1.47v)$$

Where D = distance in feet which seed will travel, S = number of seconds required for seed to fall from a height of h (ft) on a tree, and v = velocity of the prevailing wind in miles per hour.

Randall *(37)*, in a study of seed dispersal into clearcut areas, stated that at a distance of 100 m (5 chains or 330 ft) from the timber edge, the number of spruce seeds trapped were more than adequate for regeneration in a good seed year and adequate in an average year. Most of the spruce in the surrounding stands was red spruce.

Seedling Development—Most red spruce seeds germinate the spring following dispersal; some, however, may germinate in the fall soon after dropping from the tree. Germination is epigeal. On favorable seedbeds the usual spring germination period is from late May to early July. On duff, which is more subject to surface drying than most other seedbed materials, some seeds may lose viability by midsummer, and some may show delayed germination well into August *(22)*. Little if any viable seeds remain in the forest floor beyond 1 year *(13)*.

Adequate moisture is the chief factor controlling germination of red spruce. Germination takes place on almost any medium (mineral soil, rotten wood, or shallow duff) except sod. Mineral soil is an excellent seedbed for germination. Generally ample moisture is available and soil temperatures are moderate. Litter and humus are poorer seedbeds because they are likely to be hotter and drier than mineral soil *(11)*. On thicker duff, germination may be poor also because moisture conditions are less favorable. Temperatures of 20° to 30° C (68° to 86° F) are generally favorable for germination. Seeds will not germinate satisfactorily at temperatures below 20° C (68° F) and are permanently injured by long exposure to temperatures higher than 33° C (92° F) *(22)*.

Germination and initial establishment proceed best under cover. Seedlings can become established under light intensities as low as 10 percent of full sunlight; however, as they develop, they require light intensities of 50 percent or more for optimum growth. Seedlings starting in the open undergo heavy mortality when soil surface temperatures reach 46° to 54° C (115° to 130° F) even for a short time *(11)*. Drought and frost heaving are major causes of mortality the first year. Crushing by hardwood litter and snow are also causes of seedling mortality. Winter drying in some years and locations can cause severe leader damage and dieback.

Natural reproduction depends more on seedling survival than on requirements for germination. Spruce seedlings have an exceptionally slow-growing, fibrous, shallow root system. Consequently, a critical factor in their survival and establishment is the depth of the 01 organic layers of the soil profile. When the combined thickness of these layers exceeds 5 cm (2 in), spruce seedlings may not reach mineral soil and the moisture necessary to carry them through dry periods. Red spruce seedlings and the commonly associated balsam fir seedlings are similar in many ways and are controlled by the same factors, but as a rule spruce is the weaker, slower growing species during the establishment period *(22)*.

Seedlings that have attained a height of about 15 cm (6 in) can be considered established. Once established, their early growth is determined largely by the amount and character of overhead competition. Dense growth of bracken *(Pteridium aquilinum)*, raspberry, and hardwood sprouts are the chief competition for seedlings on heavily cutover lands; but red spruce survives as much as 145 years of suppression and still responds to release *(11,39)*.

Compared to its associates, red spruce is one of the last species to start height growth in the spring, usually beginning the first week in June and ending 9 to 11 weeks later. Radial growth usually begins about the second week of June and continues through August *(22)*.

Vegetative Reproduction—Red spruce rarely, if ever, layers *(15,22,45)*. Recently developed techniques facilitate propagation from stem cuttings under controlled conditions, particularly juvenile cuttings *(7,9,38,45)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Red spruce (fig. 3) is a medium-size tree at maturity, reaching 30 to 61 cm (12 to 24 in) in d.b.h. and 18 to 23 m (60 to 75 ft) in height in the Northeast, and up to 35 m (115 ft) in the Appalachian Mountains. Its maximum age is about 400 years *(22)*. The American Forestry Association lists a tree 133 cm (52.5 in) in d.b.h. and 33.5 m (110 ft) tall in Great Smoky National Park in North Carolina as the largest living red spruce.

The rate of red spruce's growth is strongly influenced by light conditions. Although trees can live in dense shade for many years, once they reach sapling to pole stage nearly full sunlight is beneficial. Understory trees no more than 1.2 or 1.5 m (4 to 5 ft) tall may be more than 50 years old, whereas trees of the same age in the open may be approaching small sawtimber size *(22)*.

Under favorable conditions, red spruce may reach an average d.b.h. of 10 cm (4 in) and height of 7 m (23 ft) in 20 years, and be over 23 cm (9 in) in d.b.h. and 19 m (62 ft) tall in 60 years *(22)*.

Diameter growth of red spruce has been related to vigor, live crown ratio (ratio of live crown to total height), live crown length, and initial diameter at breast height *(6,32)*. High vigor red spruce with a live crown ratio of 0.5 or better averaged 4.3 cm (1.7 in) of diameter growth in 10 years. Growth rates of trees with smaller crown ratios and less vigorous trees

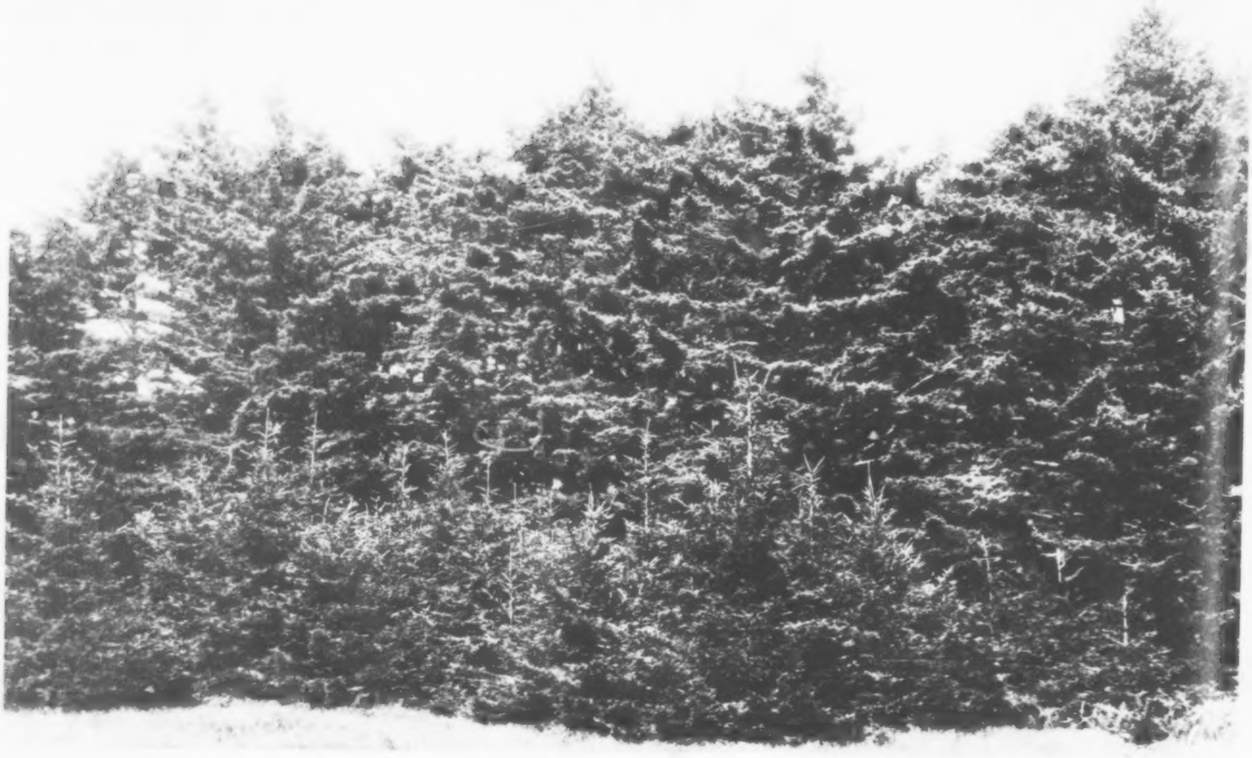

Figure 3—*Red spruce seeding into grassland on the mountains of West Virginia.*

Table 1—Classification of red spruce trees *(11)*

Tree class (rating as growing stock)	Vigor	Crown class	Live crown ratio[1]	Average 10-year growth in d.b.h.	
				cm	*in*
A. superior	I	Dominant and Intermediate	0.6+	4.6	1.8
B. good	I	Dominant and Intermediate	0.3 to 0.5	3.3	1.3
C. acceptable	II	Overtopped	0.6+		
		Intermediate	0.6+		
		Dominant	0.6+	2.3	0.9
D. inferior		Intermediate	0.3 to 0.5	1.5	0.6
E. undesirable	III	Intermediate	0.3+	0.5	0.2
		All others	0.3 or less		

[1] Ratio of live crown to total height.

decreased progressively to an average of 0.8 cm (0.3 in) in 10 years for trees of low vigor or with crown ratios smaller than 0.4 *(22)*. A tree classification for red spruce is shown in table 1 *(11)*.

In one study *(40)*, average net annual growth in softwood stands (66 to 100 percent softwood species) that can be expected from stands receiving minimal silvicultural input was found to be about 3.5 m^3/ha (50 ft^3/acre). In mixed-wood stands (21 to 65 percent softwood species) this dropped to about 2.8 m^3/ha (40 ft^3/acre), although the majority of the growth was contributed by softwoods. A further breakdown of the data shows the contributions of spruce, most of which was assumed to be red spruce, to be 51 percent in softwood stands and 39 percent in mixed-wood stands.

Yields per acre, in total volumes of all trees larger than 1.5 cm (0.6 in) in d.b.h. (inside bark and including stump and top but not butt swell), are given in table 2 *(33)*.

Table 2—Yield of red spruce by age class and site index (adapted from *33*)

Age	Site index[1]			
	12.2 m or 40 ft	15.2 m or 50 ft	18.3 m or 60 ft	21.3 m or 70 ft
yr		*m³/ha*		
20	6	8	11	14
40	94	132	164	200
60	244	335	422	507
80	308	424	533	640
100	332	456	575	691
yr		*ft³/acre*		
20	80	120	160	200
40	1,350	1,890	2,350	2,850
60	3,490	4,780	6,030	7,240
80	4,400	6,060	7,610	9,150
100	4,740	6,520	8,210	9,870

[1] Base age 50 years when age is measured at d.b.h.—total tree age is estimated to be 65 years at that time.

Table 3—Merchantable yield of red spruce (adapted from *48*)

Years since cut	Density index (regional average 100)		
	50	100	150
		m³/ha	
10	17.1	24.4	29.5
20	29.8	37.7	43.3
30	43.5	52.0	58.0
40	58.1	67.3	73.4
50	73.8	83.1	89.7
		ft³/acre	
10	245	349	422
20	425	539	618
30	622	743	828
40	830	961	1,049
50	1,054	1,187	1,281

These yields are normal yields from even-aged stands growing primarily on old fields. Therefore, they are higher than yields that might be expected from more irregular stands such as those developing after cutting *(22)*.

Site index has not been of great utility in rating the potential productivity of spruce-fir sites because of the tolerance of the species and its ability to survive in a suppressed state. Site index at base age 50 years is as good a measure of productivity as any of several growth functions, however *(39)*. Recently, polymorphic site index curves were developed for even-aged spruce and fir stands in northern Maine; they should be valuable for estimating site productivity *(20)*.

Table 4—Aboveground biomass and annual production of all tree components and foliage for red spruce at latitude 45° 30′ N. (adapted from *17*)

Moisture regime	Biomass		Annual production	
	t/ha	*tons/acre*	*t/ha*	*tons/acre*
Dry	121.3	54.1	4.5	2.0
Fresh	263.2	117.4	8.7	3.9
Moist	461.3	205.8	9.9	4.4
Wet	164.1	73.2	3.8	1.7

Other yield tables for the Northeast *(48)* take into consideration stand density, composition, and time since cutting. These tables give merchantable volume of spruce and fir combined in trees 15.2 cm (6 in) in d.b.h. and larger from a 0.3 m (1 ft) stump to a 7.6 cm (3 in) top, diameter inside bark, and are somewhat conservative. Yields of merchantable volume for different stand densities from 10 to 50 years after cutting, where 90 percent of the trees are spruce and fir growing on predominantly softwood sites, are given in table 3.

The development of stand projection growth models that permit computer simulation of red spruce tree growth for various management practices and silvicultural treatments over a range of stand conditions has flourished in recent years. For ex-

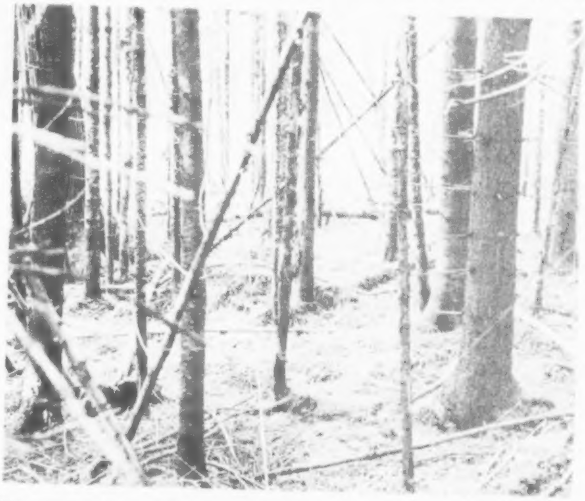

Figure 4—*A dense red spruce stand in Maine.*

ample, the model FIBER was developed in the Northeast *(43)* for spruce-fir, northern hardwood and a range of Mixedwood forest types between the two. Such models have proved very useful for forest management planning.

In recent years, interest in total biomass yield and productivity has increased, and in the future is likely to become more important in management considerations. As an example, above-ground biomass and productivity values of typical red spruce stands in Canada are given in table 4 for stands in a steady state, across a moisture regime catena *(17)*.

Rooting Habit—Spruce and fir are shallow-rooted, with most of the feeding roots in the duff and the top few centimeters of mineral soil *(11)*. The average rooting depth for all sites in Maine was found to be 33 cm (13 in), with a maximum of 56 cm (22 in) *(22)*.

Reaction to Competition—Red spruce is classified as shade tolerant in the United States and tolerant or very tolerant in Canada. Opinions differ as to whether red spruce is more tolerant than balsam fir, but the relative tolerance may vary with soil fertility and climate *(22)*.

The species' chief competition comes from balsam fir and hardwoods that produce heavy shade, like beech and maple. Competition from aspen, birch, and other thin-crowned species is not so severe. Red spruce prunes itself about as well as most softwoods in dense stands (fig. 4). As much as one-third of the live crown may be pruned artificially without seriously affecting radial growth *(5)*.

A number of studies have demonstrated the ability of red spruce to respond to release after many years of suppression. The vigor of this response does decline somewhat with age, however, and older trees may require about 5 years to recover before showing accelerated growth *(7)*. Reduction of growth to about 2.5 cm (1 in) of diameter in 25 years, for a duration of 100 years, represents about the limit of suppression for red spruce. Many of its associated tree species such as balsam fir and hemlock may outgrow red spruce after release *(22)*.

Red spruce may be grown successfully using even-age silvicultural prescriptions *(11,12)*. Red spruce is very shallow-rooted, however, making it subject to windthrow, a major silvicultural constraint in the management of the species. As a general rule, it is recommended that no more than one-fourth to one-half of the basal area be removed in the partial harvest of a spruce-fir stand, depending on site, to avoid excessive windthrow damage.

Most of the major forest cover types previously listed in which red spruce is a component are considered either climax or subclimax.

Damaging Agents—The shallow root system, thin bark, and flammable needles of red spruce make trees of all ages very susceptible to fire damage *(11)*. The acreage of red spruce originally present in the southern Appalachians has been reduced to a fraction of what it once was by fire and clearcutting *(22)*. Many former spruce sites are occupied by inferior tree species, blackberries, and ferns after 20 years *(47)*.

The most important insect enemy of red spruce is the spruce budworm, *Choristoneura fumiferana*. Although red spruce is much less vulnerable to damage than balsam fir or white spruce, largely due to later bud flushing in the spring *(3)*, much damage and mortality occur in stands containing large quantities of mature balsam fir. Blum and McLean *(4)* suggest that factors such as stand age, species composition, density, and vigor contribute to the vulnerability of spruce-fir stands to budworm damage and suggest steps to alleviate damage. Additional, detailed information may also be found in Sanders, *et al.* *(42)* for spruce-fir stands in the Northeast, the Lake States, and Canada.

The eastern spruce beetle, *Dendroctonus rufipennis*, damages mature trees of red spruce. Two species of sawflies, the European spruce sawfly, *Diprion hercyniae*, and the native yellowheaded spruce sawfly, *Pikonema alaskensis*, have severely defoliated red spruce in localized areas *(22)*. The eastern spruce gall adelgid, *Adelges abietis*, can be a serious pest on spruce when abundant. The pine leaf adelgid, *Pineus pinifoliae*, forms unsightly but relatively harmless conelike galls on red and black spruce (*Picea mariana*), which are alternate hosts *(46)*.

Red spruce has few diseases. Needle cast caused by *Lirula macrospora* may result in severe defoliation of the lower crown and a subsequent reduction of growth. *Phellinus pini* and *Phaeolus schweinitzii*, the most destructive of red spruce wood-rotting fungi, are usually confined to overmature or damaged trees. *Climacocystis borealis* causes butt rot in overmature trees *(22)*. Trees are occasionally attacked by *Armillaria mellea* and *Inonotus tomentosa*.

All along the eastern Appalachian mountain chain, from the New England states to Georgia, growth has declined in high-elevation red spruce since the 1960's *(25)*. In recent years, this decline has been accompanied by increased mortality and crown damge in high-elevation red spruce. Apparently, no significant natural biotic or abiotic causal agents have been identified, although it has been hypothesized that interaction among naturally occurring insect and disease factors and anthropogenic air pollutants, or air pollutants acting alone, are at the root of the problem. Sulphur dioxide (SO_2), nitrogen oxides (NO_x), and volatile organic compounds are the pollutants of primary concern; secondary pollutants such as ozone and nitric and sulfuric acids are also believed to be important factors *(29)*.

Growth decline and mortality in low-elevation red spruce in northern New England, while increasing in some areas, appear to be within the normal ranges for trees and forests of various ages, compositions, and density. However, some foliar symptoms have been detected in both red spruce and white pine, particularly from ozone exposure.

Red spruce is occasionally infected with eastern dwarf mistletoe, *Arceuthobium pusillum*, a parasite causing growth reduction, tree mortality, and degradation of wood quality *(24)*.

Mice and voles have been found to consume and store significant amounts of spruce seeds in preference to those of balsam fir, suggesting one reason for the low ratio of spruce to fir seedlings commonly found in naturally regenerated stands *(1,23)*. Wildlife damage to the terminal buds of young spruce, presumably by birds, also has been noted *(2)*. Some injury and mortality are also caused occasionally by porcupines, bears, deer, and yellow-bellied sapsuckers *(11)*. Red squirrels clip twigs and terminals and eat reproductive and vegetative buds *(41)*.

Special Uses

The wood of red spruce, white spruce *(Picea glauca)*, and black spruce cannot be distinguished with certainty by either gross characteristics or minute anatomy, and all three are usually marketed simply as eastern spruce. Chief uses are for lumber and pulpwood, with limited amounts going into poles, piling, boatbuilding stock, and cooperage stock *(36)*. Flakeboard and plywood have been made from spruce in recent years. It is also the preferred wood for piano sounding boards, guitars, mandolins, organ pipes, and violin bellies *(21)*.

Forest cover types that include red spruce support a wide variety of wildlife. They are particularly important as winter cover for deer and, to a certain extent, moose. Small game includes ruffed grouse, snowshoe hare, and woodcock. Many song birds and fur bearers also frequent these forest types *(44)*.

A unique use of red spruce was spruce gum, an exudate that accumulates on trunk wounds. This was the raw material for a flourishing chewing-gum industry in Maine during the last half of the 19th century and early years of this century *(21)*.

Genetics

Successful interspecific crosses with *Picea rubens* as male or female parents have been reported or confirmed for *P. mariana*, *P. omorika*, *P. glehnii*, *P. orientalis*, and *P. koyamai (15)*; *P. sitchensis (14)*; *P. glauca*, *P. mexicana (16)*; *P. × lutzii* Little *(P. sitchensis × P. glauca)*, *P. maximowiczii*, and *P. likiangensis (19)*.

Crossability of *P. rubens* with *P. omorika* is good with *P. mexicana* and *P. likiangensis* moderate; with *P. mariana*, *P. orientalis*, *P. maximowiczii*, and *P. glehnii* fair to poor; and with *P. koyamai*, *P. sitchensis*, *P. × lutzii*, and *P. glauca* very poor. Several species fail to cross with *P. rubens (15,16,18,19)*.

Hybrids between *P. rubens* and *P. mariana* occur to some extent in nature, but parental species remain phenotypically pure in their characteristic habitats *(15,30,31,34,35)*.

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Picea sitchensis (Bong.) Carr. Sitka Spruce

Pinaceae Pine family

A. S. Harris

Sitka spruce *(Picea sitchensis)*, known also as tideland spruce, coast spruce, and yellow spruce, is the largest of the world's spruces and is one of the most prominent forest trees in stands along the northwest coast of North America. This coastal species is seldom found far from tidewater, where moist maritime air and summer fogs help to maintain humid conditions necessary for growth. Throughout most of its range from northern California to Alaska, Sitka spruce is associated with western hemlock *(Tsuga heterophylla)* in dense stands where growth rates are among the highest in North America. It is a valuable commercial timber species for lumber, pulp, and many special uses *(15,16)*.

Habitat

Native Range

Sitka spruce (fig. 1) grows in a narrow strip along the north Pacific coast from latitude 61° N. in southcentral Alaska to 39° N. in northern California. The most extensive portion of the range in both width and elevation is in southeast Alaska and northern British Columbia, where the east-west range extends for about 210 km (130 mi) to include a narrow mainland strip and the many islands of the Alexander Archipelago in Alaska and the Queen Charlotte Islands in British Columbia *(24)*. North and west of southeast Alaska, along the Gulf of Alaska to Prince William Sound, the range is restricted by steep mountains and piedmont glaciers edging the sea. Within Prince William Sound, the range again widens to about 105 km (65 mi) to include many offshore islands. Westward, the range again narrows. It extends across Cook Inlet to Cape Kubugakli and across Shelikof Strait to the islands of the Kodiak Archipelago where the range continues to advance to the southwest.

In southern British Columbia, the range includes a narrow mainland strip and offshore islands, but the best development occurs on the northern tip and west side of Vancouver Island. On the east side of Vancouver Island and on the mainland south to Washington, the range tends to be restricted to seafacing slopes and valley bottoms.

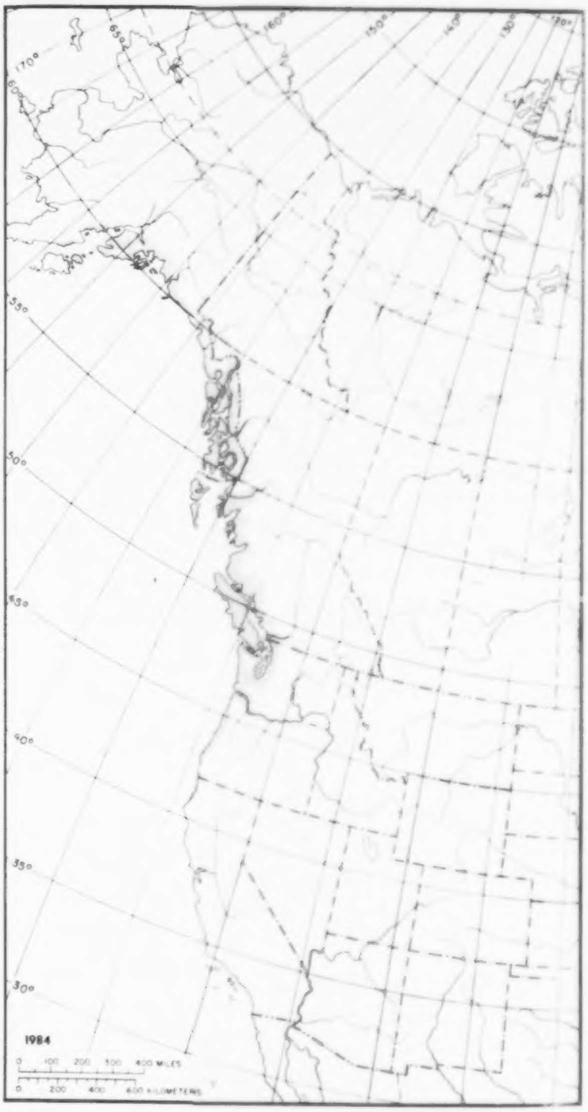

Figure 1—*The native range of Sitka spruce.*

In Washington, the range includes a narrow mainland strip along the Strait of Georgia, around Puget Sound, up valleys to the east, and on the Olympic Peninsula. On the west side of the Olympic Peninsula, the range broadens to include the extensive

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coastal plain and seaward mountain slopes. It narrows southward along the Washington and Oregon coast but extends inland for several kilometers along the major rivers. In northern California, the range is more attenuated and becomes discontinuous. A disjunct population in Mendocino County, CA, marks the southern limit of the range.

Climate

Sitka spruce is restricted to an area of maritime climate with abundant moisture throughout the year, relatively mild winters, and cool summers. Summer temperatures decrease northward and lack the extremes found in more continental locations. In terms of growing degree days, annual heat sums (based on a threshold of 5° C or 41° F) range from 2511° C (4,552° F) at Brookings, OR (lat. 41° 03′ N.) to 851° C (1,564° F) at Cordova, AK (lat. 60° 30′ N.) *(8)*. The number of frost-free days varies locally but generally declines northward; averages range from about 294 days at Brookings, OR, to 111 days at Cordova, AK.

Annual precipitation varies within the range of Sitka spruce and is influenced greatly by local topography. Annual precipitation of 2950 mm (116 in) at Forks, WA, and 5615 mm (221 in) at Little Port Walter, AK, contrasts with 635 mm (25 in) at Anacortes, WA, and 660 mm (26 in) at Skagway, AK. Summer precipitation is greater toward the north, where light drizzle and fog are frequent. At Cordova, AK, from June to September, at least a trace of precipitation occurs during 22 to 24 days each month. In contrast, at Otis, OR, a trace or more of precipitation occurs on only 8 to 15 days each month. Toward the south, fog and moist maritime air are important in maintaining moisture conditions needed for growth; most winter precipitation is in the form of rain. Depth of snowfall increases northward. Average annual snowfall at sea level is 1 cm (0.5 in) at Brookings, OR; 58 cm (23 in) at Quatsino, BC; and 340 cm (134 in) at Cordova, AK.

Soils and Topography

Sitka spruce grows on Entisols, Spodosols, Inceptisols, and Histosols, on soils derived from a wide variety of parent material. The species requires relatively high amounts of available calcium, magnesium, and phosphorus, and grows best where soils are derived from rocks rich in calcium and magnesium *(19)*. Best development is on deep, moist, well-aerated soils. Drainage is an important factor, and growth is poor on swampy sites. Sitka spruce commonly occupies alluvial soils along streams, sandy or coarse-textured soils, or soils having a thick accumulation of organic material. Soils are usually acidic, and pH values of 4.0 to 5.7 are typical. Spruce is an early pioneer on immature soils recently exposed by glacial retreat or uplift from the sea. It is more tolerant of ocean spray than are associated trees and often occupies a prominent position on exposed headlands and beaches along the outer coast *(2)*. In Oregon and Washington, spruce follows lodgepole pine *(Pinus contorta)* in succession on coastal sand dunes as they become stabilized by vegetation. On highly disturbed sites, it frequently becomes established concurrently with red alder *(Alnus rubra)* or Sitka alder *(A. sinuata)*, gradually succeeding the alder as stands are eventually overtopped.

Sitka spruce grows from sea level to treeline in Alaska, at elevations ranging from 910 m (3,000 ft) in southeast Alaska to 300 m (1,000 ft) in Prince William Sound. High mountains of the coast ranges lie close to the sea, forming a barrier to moist, onshore winds and providing abundant moisture during the growing season. Spruce is limited in elevation by the short growing season at treeline. South of northern British Columbia, spruce is restricted to low elevations near the sea where moist maritime air and fog help provide moisture during summer. For the most part, high mountains that otherwise might offer suitable habitat lie farther inland where more continental conditions of summer drought and warmer temperatures are unsuitable for growth. Exceptions are on the Olympic Peninsula and in valleys in the Cascade Range off Puget Sound in Washington, and on isolated peaks in Oregon. On the Olympic Peninsula, Sitka spruce rarely grows above 610 m (2,000 ft) in elevation *(1)*.

Associated Forest Cover

Sitka spruce is commonly associated with western hemlock throughout most of its range (fig. 2). Toward the south, other conifer associates include Douglas-fir *(Pseudotsuga menziesii)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, western white pine *(Pinus monticola)*, and redwood *(Sequoia sempervirens)*. Shore pine *(P. contorta* var. *contorta)* and western redcedar *(Thuja plicata)* are also associates that extend into southeast Alaska. Toward the north, conifer associates also include Alaska-cedar *(Chamaecyparis nootkatensis)*, mountain hemlock *(Tsuga mertensiana)*, and subalpine fir *(Abies lasiocarpa)*—trees that are usually found only at higher elevations toward the south. In central and northern British Columbia and Alaska, however, these species are found with Sitka spruce from sea level to timberline. White spruce *(Picea glauca)* is also associated with Sitka spruce in Alaska, and hybrids occur. The most important hardwood associates are red alder and bigleaf maple (*Acer macrophyllum*) in the south and red alder and Sitka alder toward the north. Black cottonwood (*Populus trichocarpa*) is an associate throughout the range.

Stands stocked with at least 80 percent Sitka spruce are identified as the forest cover type Sitka Spruce (Society of American Foresters Type 223) *(6)*. Sitka spruce is also a component of 10 other forest cover types:

221	Red Alder
222	Black Cottonwood–Willow
224	Western Hemlock
225	Western Hemlock-Sitka Spruce
227	Western Redcedar–Western Hemlock
228	Western Redcedar
229	Pacific Douglas-Fir
230	Douglas-Fir–Western Hemlock
231	Port-Orford-Cedar
232	Redwood

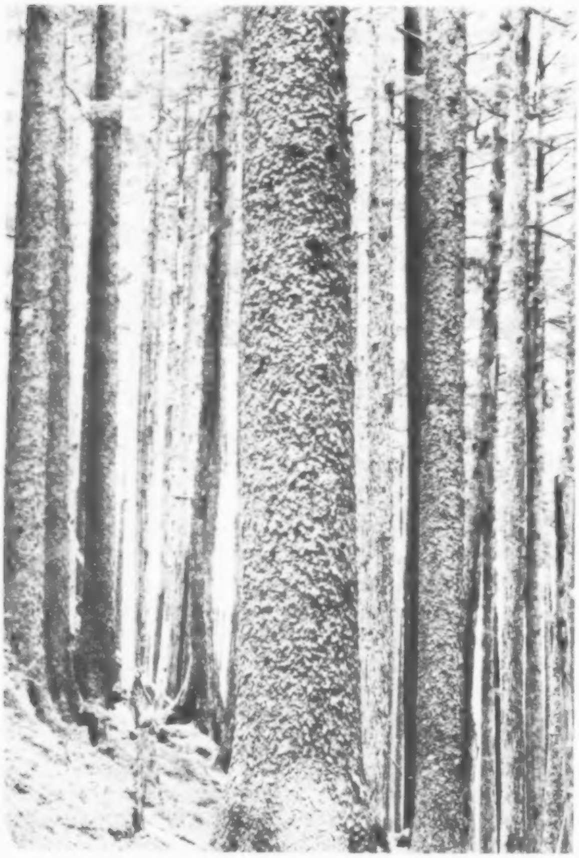

Figure 2—*Sitka spruce about 200 years old in an even-aged western hemlock—Sitka spruce stand near Ketchikan, AK. Average diameter of spruce is 91 cm (36 in); average diameter of hemlock, 56 cm (22 in).*

Sitka spruce usually grows in mixed stands, less often in pure stands. Pure stands usually occur in early successional situations and as tidewater stands influenced by salt spray. The most extensive pure stands are found on the Kodiak-Afognak Archipelago at the extreme west extension of the range. Sitka spruce is the only conifer present on this group of islands. A relatively recent invader there, spruce is expanding its range to the southwest, invading a tundra complex at the rate of about 1.6 km (1 mi) per century *(14)*.

In Oregon and Washington, common understory species associated with Sitka spruce include swordfern (*Polystichum munitum*), Oregon oxalis (*Oxalis oregana*), false lily-of-the-valley (*Maianthemum dilatatum*), western springbeauty (*Montia sibirica*), three-leaved coolwort (*Tiarella trifoliata*), evergreen violet (*Viola sempervirens*), stream violet (*V. glabella*), Smith fairybells (*Disporum smithii*), red huckleberry (*Vaccinium parvifolium*), and rustyleaf menziesia (*Menziesia ferruginea*). On drier sites, salal (*Gaultheria shallon*), Pacific rhododendron (*Rhododendron macrophyllum*), and evergreen huckleberry (*Vaccinium ovatum*) are common. On wetter forest sites, the previously mentioned species are found, along with devilsclub (*Oplopanax horridum*), ladyfern (*Athyrium filix-femina*), deerfern (*Blechnum spicant*), mountain woodfern (*Dryopteris austriaca*), and Pacific red elder (*Sambucus callicarpa*) *(11)*.

In Alaska, the more common understory plants include devilsclub, skunkcabbage (*Lysichitum americanum*), ovalleaf huckleberry (*Vaccinium ovalifolium*), red huckleberry, Alaska blueberry (*V. alaskaense*), rustyleaf menziesia, salmonberry (*Rubus spectabilis*), five-leaf bramble (*R. pedatus*), thimbleberry (*R. parviflorus*), bunchberry (*Cornus canadensis*), stink currant (*Ribes bracteosum*), and trailing black currant (*R. laxiflorum*) *(32)*. Cryptogams are abundant throughout the range of Sitka spruce. The Olympic Peninsula is especially noted for mosses, many of which occur as epiphytes on living trees.

In Oregon and Washington within the Sitka spruce forest zone, important plant communities include *Tsuga heterophylla–Picea sitchensis/Gaultheria shallon/Blechnum spicant, Tsuga–Picea/Oplopanax horridum/Athyrium filix-femina,* or *Tsuga–Picea/Polystichum munitum–Oxalis oregana (11)*. Similar communities can be found in southern British Columbia within the "fog western hemlock/Sitka spruce subzone" *(23)*. In Alaska, some of the more common communities include *Picea sitchensis/Oplopanax horridum–Rubus spectabilis/Cornus canadensis, Picea sitchensis–Tsuga heterophylla/Lysichiton americanum/Sphagnum* spp., and *Tsuga heterophylla–Picea sitchensis–(Thuja plicata)/Vaccinium ovalifolium–V. alaskaense/Rhytidiadelphus loreus (32)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Individual Sitka spruce may occasionally produce cones before 20 years of age, but cone bearing in stands usually does not begin until ages 20 to 40 *(24)*. Sitka spruce is monoecious; female strobili (cones) are usually produced at the ends of primary branches near tops of trees; male strobili are usually produced at the ends of secondary branches lower in trees. Both may be on the same branch. Reproductive buds are initiated in early summer of the year preceding pollination and seed ripening, and heavy cone crops have been explained in terms of early summer drought the preceding year. Cones ripen in the year they were pollinated. Pollen is shed from the last week in April in the southern portion of the natural range through early June in the extreme northwest part of the range. Time of flowering is mainly related to temperature.

Seed Production and Dissemination—Seeds of Sitka spruce are small, averaging 463,000/kg (210,000/lb) *(26)*. Seeds ripen in southeast Alaska during late August or early September, and dispersal usually begins in October. Cones open during dry weather, release seed, and reclose during wet weather. One study showed that 73 percent of the seed was released within 6 weeks of the first dispersal date, and the remainder was released over 1 year *(15)*. Good crops occur at 3- to 5-year intervals in the southern part of the range and at 5- to 8-year intervals in Alaska. Cone and seed production in seed orchards can be increased by treating trees with gibberellin *(31)*. Dispersal distance depends on several factors, including height and location of the seed source, local topography, and wind conditions. Reported dispersal distances range from 0.8 km (0.5 mi) when a seed source was on high ground, to 30 m (100 ft) when seed was released from the edge of a clearcut area *(15)*.

Seedling Development—Under natural conditions, seed germinates on almost any seedbed, but survival may be low. Germination is epigeal *(26)*. A mineral soil or mixed mineral and organic soil seedbed is usually considered best for germination, especially under light shade, as long as drainage is adequate and the soil provides sufficient nutrients for tree growth. Fine-textured soils combined with a high water table are suitable for germination but may be unsuitable for seedling establishment because of frost heaving. Coarse-textured mineral soils in unshaded conditions may dry out excessively but may improve after invasion by hair mosses that bind the soil surface and provide shade. Organic seedbeds are suitable in shade but are unsuitable in the open if subject to severe moisture fluctuations. On alluvial sites having high water tables and subject to frequent flooding, where competition from brush is severe, rotten wood may be the only suitable seedbed.

Vegetative Reproduction—Asexual reproduction by layering occurs under natural conditions and in plantations, but layering is most likely to occur on very moist sites at the edges of bogs or near timberline. Asexual propagation can be done by air-layering or rooting of stem cuttings. Clones differ in their ability to root or graft, and clones that graft easily do not necessarily root easily and vice versa. Cuttings from shoots of the current year root more easily than cuttings from older branches *(15)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Height growth is slow for the first few years but increases rapidly thereafter (fig. 3). On average sites in southeast Alaska, trees can be expected to reach about 27 m (90 ft) in height within 50 years after attaining breast height *(7)*. Average site index at elevations near sea level varies inversely with latitude, declining from 48 m (158 ft) at base age 100 years in Lincoln County, OR, to 33 m (108 ft) in southeast Alaska, at the rate of about 1 m (3 ft) per degree of latitude *(8)*. Observations within the natural range of spruce show that growth rate also declines with increasing elevation.

Height growth of Sitka spruce and western hemlock are nearly equal during the period of most rapid growth, but spruce grows more rapidly in diameter. Consequently, thinning from below tends to favor spruce. Spruce continues to maintain height growth longer than hemlock and lives longer. Few hemlock live more than 500 years; Sitka spruce may live to 700 or 800 years. Very old spruces eventually assume a dominant position in old-growth hemlock-spruce stands.

Sitka spruce trees often attain great size. In Alaska, mature trees near sea level may exceed 61 m (200 ft) in height and 3 m (10 ft) in d.b.h. In Oregon, a tree 87 m (286 ft) tall was reported *(24)*. The largest tree on record is located near Seaside, OR. It is 5.1 m (16.7 ft) in d.b.h. and 65.8 m (216 ft) tall and has a crown spread of 28 m (93 ft) *(17)*.

Stands in which Sitka spruce is a major component tend to be dense, and yields are high *(21,30)*. Stand volumes can be impressive. One plot in a 147-year-old hemlock-spruce stand in coastal Oregon contained, on an area basis, 188 spruce and 32 hemlock/ha (76 spruce and 13 hemlock/acre). Total volume was 2380 m^3/ha (34,000 ft^3/acre). Spruce averaged 64 m (210 ft) in height and 86 cm (34 in) in d.b.h., and hemlock averaged 44 m (144 ft) in height and 46 cm (18 in) in d.b.h *(24)*.

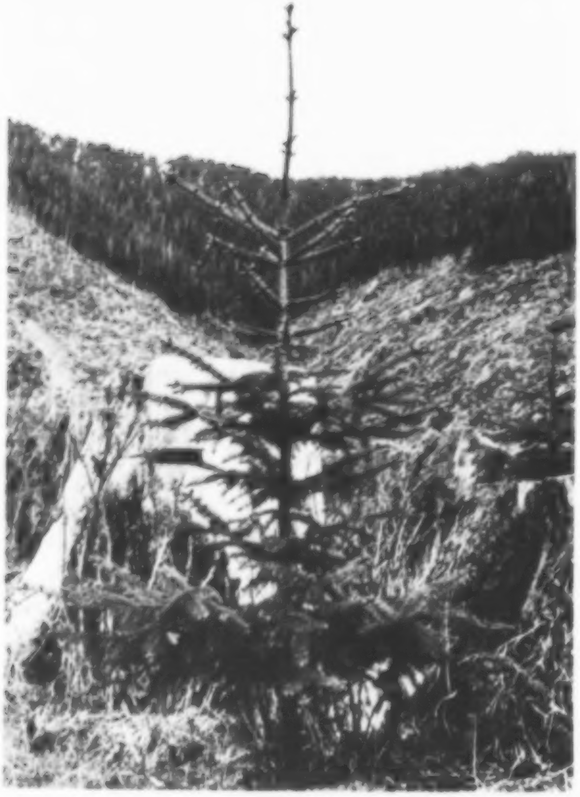

Figure 3—*Natural regeneration of Sitka spruce 10 years after a western hemlock-Sitka spruce stand was clearcut in Maybeso Valley, southeast Alaska.*

Rooting Habit—Roots will grow where moisture, fertility, aeration, and mechanical soil properties are favorable. Consequently, there is great variability in root form—from flat platelike roots to deep, narrow-spreading roots *(12)*. Where soils are shallow, soil temperature and fertility low, and water tables high, shallow rooting is by far the most common form. Deeper rooting does occur, however, where soils have good drainage and depth to water table. Rooting to depths of 2 m (6 ft) has been reported *(5)*.

Sitka spruce commonly produces long lateral roots with few branches and rapid elongation *(20)*. Annual elongation rates of 42 to 167 cm (16 to 66 in) have been reported *(3)*. Lateral roots up to 23 m (75 ft) in length have been observed in Alaska *(15)*. Root grafting occurs between roots of the same tree and between adjacent trees. It is fairly common to find living stumps sustained by root grafts from adjacent trees. Adventitious roots develop on trees growing along streams where alluvium is deposited by periodic flooding. Roots are vulnerable, however, to compaction and lack of aeration. Spruce are frequently killed by permanent flooding caused by beavers, and often valuable ornamental and roadside trees are killed when landfill is deposited around them. Containerized nursery stock has been successfully inoculated with the mycorrhizal fungi, *Laccaria laccata* and *Cenococcum geophilum (29)*.

Reaction to Competition—Sitka spruce is more tolerant of shade than Douglas-fir but less tolerant than hemlock. Depending on latitude, Sitka spruce has been described as being in the tolerant and intermediate shade-tolerant classes. Overall, it probably can most accurately be classed as tolerant of shade. Since reproduction under mixed stands is predominantly hemlock, there is a tendency for this more tolerant species to eventually dominate the site. Few climax stands proceed to pure hemlock, however; in time, small openings, usually caused by blowdowns, develop, allowing reproduction of spruce. The combination of greater stature, greater longevity, and occasional stand disturbance is enough to assure a scattering of spruce in the overstory of most climax hemlock-spruce stands (fig. 4).

Sitka spruce is one of the few conifers that develop epicormic branches along the stem. Production of these sprouts is related to light intensity, and roadside trees often develop dense new foliage from base to crown. Thinning stimulates epicormic branching and could decrease the quality of the wood, although this is not a problem in production of pulp or dimension lumber. In deep shade, lower limbs soon die, decay, and break off, but the resinous branch stubs remain for many years.

Damaging Agents—Blowdown is probably the most serious damaging agent of Sitka spruce, but the species is attacked by a number of pests—insects, disease organisms, and animals. In general, problems tend to be more severe toward the south. The white pine weevil (*Pissodes strobi*) is the most serious insect pest in Oregon, Washington, and southern British Columbia; weevil damage has been the most serious deterrent to management of Sitka spruce in the southern part of its range. Damage is most severe on young trees 3 to 6 m (10 to 20 ft) tall. The weevil is not a problem on the Queen Charlotte Islands or in Alaska, possibly because there is insufficient summer heat to allow its development *(22)*. The spruce aphid (*Elatobium abietinum*) feeds on Sitka spruce from California to Alaska and is a pest of ornamental trees. Epidemics are sporadic and short lived. A root-collar weevil (*Steremnius carinatus*) girdles 1- and 2-year-old seedlings, causing some losses. The spruce beetle (*Dendroctonus rufipennis*) periodically damages stands throughout the range and is a major pest of spruce in British Columbia. In addition, damage from a number of defoliators and other insects is common *(13)*.

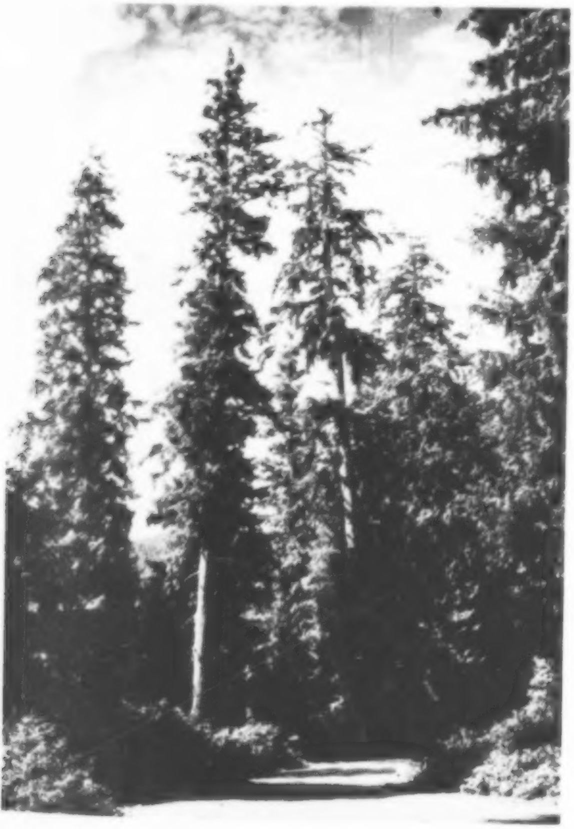

Figure 4—*Sitka spruce trees, north of Ketchikan, AK, 46 m (150 ft) tall and 1.8 to 2.1 m (6 to 7 ft) in d.b.h.*

Sitka spruce is highly susceptible to decay when injured *(18)*. In the past, most emphasis has been on studies of decay in old-growth stands, but currently interest is shifting to young, managed stands. Some of the organisms causing decay in old growth (for example, *Heterobasidion annosum* and *Armillaria mellea*) can also cause root rot in young stands. *Heterobasidion annosum* infects freshly cut stump surfaces, and in Europe the tendency for plantation-grown Sitka spruce to develop *H. annosum* butt rot is well known.

Foliage and stem diseases are usually of minor importance. Several rusts cause occasional light to moderate defoliation, witches' brooms, or loss of cones. Seed and seedling diseases are probably most important in production of containerized seedlings in greenhouses.

Sitka spruce is damaged at various locations by animals such as elk, bear, deer, porcupines, rabbits, hares, and squirrels. In general, these problems are more serious in the southern part of the range. Deer are generally more troublesome in the southern part, porcupines in the northern part *(25)*. Spruce is often less damaged than its associates.

Few growth abnormalities have been reported, although large tumorlike growths on stems have been reported in Washington, and they occur in Alaska as well. The causal agent is not known.

Special Uses

High strength-to-weight ratio and resonant qualities of clear lumber are attributes that have traditionally made Sitka spruce wood valuable for specialty uses, such as sounding boards for high-quality pianos; guitar faces; ladders; construction components of experimental light aircraft; oars, planking, masts, and spars for custom-made or traditional boats; and turbine blades for wind energy conversion systems.

Genetics

In addition to the clinal latitudinal difference in growth rate, cone characteristics such as size, length-to-width ratio, angle of sterigma, and phylotaxy also vary with latitude *(4)*.

Variation in wood characteristics has been reported by provenance, region, site, and individual trees. Although no comprehensive heritability studies have been completed, Sitka spruce shows considerable variation in wood density, tracheid length, and grain angle. Improvement in these characteristics through breeding appears feasible. Selection for vigor tends to favor trees of lower-than-average specific gravity but has no effect on tracheid length *(15)*.

Provenance studies show that—at a given planting site—northern, inland, and high-elevation sources are the first and the most variable in breaking dormancy. Dormancy appears to be influenced by photoperiod, and northern provenances are the first to enter dormancy. Total seasonal height growth is positively correlated with the time interval between flushing and dormancy. When moved north, introduced southern sources make better height growth, but they may be subject to frost damage if moved too far or planted on exposed sites. Once dormant, Sitka spruce is able to endure very low temperatures without damage. Sitka spruce from northern provenances may be more resistant to freezing than those from southern provenances. Dormant leaves from a Bellingham, WA, source withstood temperatures to -30° C (-22° F), whereas a Juneau, AK, source withstood temperatures to -40° C (-40° F). Twigs of the two sources withstood temperatures to -40° C and -60° C (-40° F and -76° F), respectively *(27)*.

Only limited data are available on genetic variation between individual trees. Assessment of first-year characteristics of progeny from a diallel cross among six trees showed that characters affecting tree form were inherited in a predominantly additive fashion; characters reflecting tree vigor were under "additive, dominance, and maternal control" *(28)*. Self-pollinated progeny showed growth depression caused by inbreeding *(28)*.

Population Differences

Biochemical variation between populations of Sitka spruce from various parts of its natural range has been studied for polyphenols, isoenzymes, and terpenoids. Differences in polyphenol concentrations have been found between different origins, and a high degree of variation in monoterpene concentrations has been shown between trees in stands and by stand origin. Polyphenol, isoenzyme, and terpenoid analyses have been used in studying the introgression between Sitka spruce and white spruce *(9)*.

Variation is known to occur within the cell nucleus. The length of the haploid complement and the nuclear volume increase with latitude of seed origin. Seeds from northern sources have more DNA per cell than those from southern provenances. Supernumerary (B) chromosomes have been found in seeds from eight provenances *(15)*.

Genetic tree improvement programs are progressing in Britain and in Denmark. In North America, efforts toward tree improvement have been concerned primarily with developing procedures for control of indiscriminate transfer of seeds and plant materials. Efforts are being made to locate plus-trees, primarily by private industrial forest organizations, and seed orchards are being established.

Hybrids

A natural hybrid between Sitka spruce and white spruce *(Picea × lutzii* Little) occurs in the Skeena River Valley, BC, and on the Kenai Peninsula, AK. The hybrid shows some resistance to the white pine weevil. Sitka spruce is also known to cross with Yezo spruce *(Picea jezoensis)*, Serbian spruce *(P. omorika)*, and Engelmann spruce *(P. engelmannii) (33)*. The cross black spruce *(Picea mariana* × Sitka spruce) on black spruce strobili has yielded viable seed. Crossability averaged 5 percent; this low average suggests that black spruce does not share the same phylogenetic relationship with the more easily crossed Sitka, white, and Engelmann spruces *(10)*.

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Pinus albicaulis Engelm. Whitebark Pine

Pinaceae Pine Family

Stephen F. Arno and Raymond J. Hoff

Whitebark pine (*Pinus albicaulis* Engelm.) is a slow-growing, long-lived tree of the high mountains of southwestern Canada and western United States. It is of limited commercial use, but it is valued for watershed protection and esthetics. Its seeds are an important food for grizzly bears and other wildlife of the high mountains. Concern about the species has arisen because in some areas whitebark pine cone crops have diminished as a result of successional replacement and insect and disease epidemics *(6,48)*.

Habitat

Native Range

Whitebark pine (fig. 1) grows in the highest elevation forest and at timberline. Its distribution is essentially split into two broad sections, one following the British Columbia Coast Ranges, the Cascade Range, and the Sierra Nevada, and the other covering the Rocky Mountains from Wyoming to Alberta.

Whitebark pine is abundant and vigorous on the dry, inland slope of the Coast and Cascade Ranges. It is absent from some of the wettest areas, such as the mountains of Vancouver Island. In the Olympic Mountains, it is confined to peaks in the northeastern rain shadow zone. Whitebark pine also occurs atop the highest peaks of the Klamath Mountains of northwestern California.

The Rocky Mountain distribution extends along the high ranges in eastern British Columbia and western Alberta, and southward at high elevations to the Wind River and Salt River Ranges in west-central Wyoming.

A small outlying population of whitebark pine is found atop the Sweetgrass Hills in north-central Montana 145 km (90 mi) east of the nearest stands in the Rocky Mountains across the Great Plains grassland *(73)*.

The coastal and Rocky Mountain distributions lie only 100 km (62 mi) apart at their closest proximity *(10)*. Even this narrow gap is not absolute; small groves are found on a few isolated peaks in between in northeastern Washington. In addition to the main distribution, whitebark pine grows in the Blue and Wallowa Mountains of northeastern Oregon and in several isolated ranges rising out of the sagebrush steppe in northeastern California, south-central Oregon, and northern Nevada.

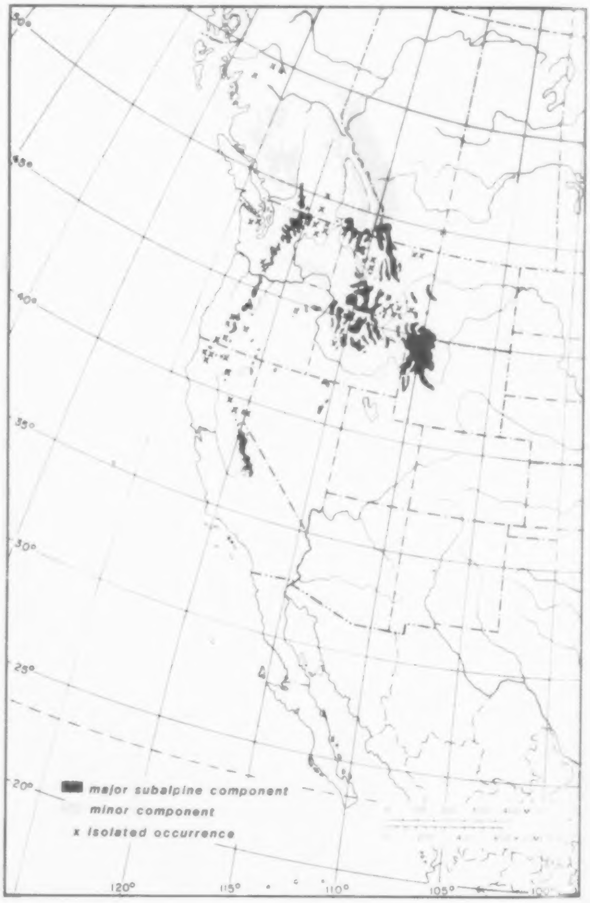

Figure 1—*Natural distribution of whitebark pine, revised from Little (53).*

Climate

Whitebark pine grows in a cold, windy, snowy, and generally moist climatic zone. In moist mountain

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ranges, whitebark pine is most abundant on warm, dry exposures. Conversely, in semiarid ranges, it becomes prevalent on cool exposures and moist sites. Weather data from several whitebark pine sites in the Inland Northwest suggest the climatic interpretations that follow *(3,83)*. Summers are short and cool with mean July temperatures ranging from 13° to 15° C (55° to 59° F) in the whitebark pine forest and from 10° to 12° C (50° to 54° F) in the adjacent timberline zone. A cool growing season, as defined by mean temperatures higher than 5.5° C (42° F) *(11)*, lasts about 90 to 110 days in the whitebark pine forest, but light frosts and snowfalls sometimes occur even in mid-summer. The hottest summer days reach temperatures of 26° to 30° C (79° to 86° F). January mean temperatures range from about –9° C (15° F) in Montana to about –5° C (23° F) in the Cascades and Sierra Nevada. Long-term record low temperatures in Montana and Wyoming stands are probably –40° to –50° C (–40° to –58° F).

Mean annual precipitation for most stands where whitebark pine is a major component probably is between 600 and 1800 mm (24 and 72 in). The lower part of this precipitation range applies to mountain ranges in semiarid regions where whitebark pine forms nearly pure stands or is accompanied only by lodgepole pine *(Pinus contorta* var. *latifolia)*. The highest precipitation occurs in inland-maritime ranges and near the Cascade crest where whitebark pine grows primarily with subalpine fir *(Abies lasiocarpa)* and mountain hemlock *(Tsuga mertensiana)*.

About two-thirds of the precipitation in most stands is snow and sleet, with rain prevailing only from June through September *(3)*. Summer rainfall is often scant in the southern part of whitebark pine's distribution south of about 47° N. latitude. Thus, there is often a droughty period with scant rainfall or remaining snowmelt water for several weeks during mid- to late-summer.

Snowpack usually begins to accumulate in late October. By April, the snowpack reaches maximum depth, ranging from about 60 to 125 cm (24 to 50 in) in stands east of the Continental Divide and in other semiarid areas, to 250 to 300 cm (100 to 120 in) in the relatively moist whitebark pine–subalpine fir stands of the Cascades and inland-maritime mountains. Most stands probably have mean annual snowfalls between 460 and 1270 cm (180 and 500 in). Whitebark pine also grows in stunted or krummholz (shrub-like) form on windswept ridgetops where little snow accumulates.

Strong winds, thunder storms, and severe blizzards are common to whitebark pine habitats. Wind gusts of hurricane velocity in the tree crowns (more than 117 km/h or 73 mi/h) occur each year on most sites, but most frequently on ridgetops.

Soils and Topography

Most whitebark pine stands grow on weakly developed (immature) soils. Many of the sites were covered by extensive mountain glaciers during the Pleistocene and have been released from glacial ice for less than 12,000 years *(62)*. Chemical weathering is retarded by the short, cool, summer season. Also, nitrogen-fixing and other microbiotic activity that might enrich the soil is apparently restricted by low soil temperature and high acidity on many sites.

Despite these general trends, substantial variations occur in local climates, geologic substrates, and degrees of soil development in whitebark pine habitats. Thus, several types of soils have been recognized.

Most soils under whitebark pine stands are classified as Inceptisols *(82)*. Many of these are Typic Cryochrepts, although deposits of volcanic ash may be sufficiently thick in some profiles to warrant recognition as Andic Cryochrepts. Some of the best-developed, ash-layered soils beneath spruce-fir–whitebark pine stands are Typic Cryandepts similar to the zonal Brown Podzolic soils *(64)*. All of these are young soils, showing less leaching, weathering, and horizon development than Spodosols, although they are strongly acidic. Mean pH values of 4.8 to 5.0 were found for the upper mineral soil horizons in three habitat types, probably composed largely of Typic Cryochrepts *(66)*. Data on nutrient availability in these soils have been provided *(83)*.

Throughout its distribution, whitebark pine is often found on soils lacking fine material. Sparse open stands often grow on coarse talus, exposed bedrock, or lava flows having minimal horizon development and only scattered pockets of fine material. These soils would be classified as fragmental and loamy skeletal families within the order Entisols (Cryorthents in granitic substrates) *(82)*. They have been referred to as azonal soils, and more specifically as Lithosols in earlier classifications.

Some dry-site whitebark pine stands in semiarid regions have open, grassy understories, particularly on calcareous rock substrates. The soils have a thick, dark surface horizon and a nearly neutral reaction. The pH is near 6 in Montana *(66)* and Idaho *(71)* stands, but in Alberta average values are 7.8 to 8 *(9)*. These soils would evidently be classified as Typic Cryoborolls within the order Mollisols *(82)*. Also, in some of the same areas, soils that have a dark surface but low base saturation are classified as Typic Cryumbrepts.

In all but the driest regions, whitebark pine is most abundant on warm aspects and ridgetops having direct exposure to sun and wind. It is less abundant on sheltered, north-facing slopes and in cirque basins, where subalpine fir, Engelmann spruce *(Picea engelmannii)*, mountain hemlock, or alpine larch *(Larix lyallii)* become prevalent. Nevertheless, the tallest and best formed whitebark pine trees are often found in high basins or on gentle north slopes.

Near the northern end of its distribution in the British Columbia coastal mountains, whitebark pine is a minor component of timberline communities at about 1580 m (5,200 ft) elevation *(58)*. In the Olympic Mountains and on the western slope of the Cascades in Washington and northern Oregon, it grows primarily on exposed sites near tree line between 1770 and 2130 m (5,800 and 7,000 ft). (Elevational ranges mentioned are mostly from *7)*. East of the Cascade crest it becomes abundant within both the subalpine forest and the timberline zone. For instance, it is common between 1620 and 2440 m (5,300 and 8,000 ft) in central Washington's Stuart Range, generally forming krummholz above 2130 m (7,000 ft). The lowest reported natural stand of whitebark pine throughout its range is at 1100 m (3,600 ft) near Government Camp on the southwest slope of Mount Hood in Oregon *(28)*.

Whitebark pine becomes a major component of high-elevation forests in the Cascades of southern Oregon and northern California, growing between 2440 and 2900 m (8,000 and 9,500 ft) on Mount Shasta. In the central and southern Sierra Nevada it is found between 3050 and 3510 m (10,000 and 11,500 ft) but occasionally reaches 3660 m (12,000 ft) as krummholz cushions.

Near the north end of its distribution in the Rockies of Alberta and British Columbia, whitebark pine is generally small, scattered, and confined to dry, exposed sites at timberline, 1980 to 2290 m (6,500 to 7,500 ft). It becomes increasingly abundant southward, especially in Montana and central Idaho. It is a major component of high-elevation forests and the timberline zone between about 1800 and 2500 m (5,900 and 8,200 ft) in northwestern Montana and 2130 and 2830 m (7,000 and 9,300 ft) in west-central Montana. In western Wyoming, it is abundant at 2440 to 3200 m (8,000 to 10,500 ft).

Associated Forest Cover

Whitebark pine is most frequently found growing with other high mountain conifers, although pure whitebark pine stands are common in dry mountain ranges. The forest cover type Whitebark Pine (Society of American Foresters Type 208) *(70)* is used to designate pure stands or mixed stands in which the species comprises a plurality. Whitebark pine is also a minor component of Engelmann Spruce–Subalpine Fir (Type 206) in the Rockies, eastern Cascades, and the Blue Mountains; Mountain Hemlock (Type 205) in much of the Cascades and British Columbia coastal mountains; and California Mixed Subalpine (Type 256) in the California Cascades, Sierra Nevada, and Klamath Mountains. In these open, upper subalpine forests, whitebark pine is associated with mountain hemlock, California and Shasta red fir *(Abies magnifica* vars. *magnifica* and *shastensis)*, Sierra lodgepole pine *(Pinus contorta* var. *murrayana)*, western white pine *(P. monticola)*, and locally, foxtail *(P. balfouriana)* and limber *(P. flexilis)* pines.

In the dry ranges of the Rockies south of latitude 47° N. and in south-central Oregon, whitebark pine is found within the highest elevations of the cover type Lodgepole Pine (Type 218). In the Rockies, whitebark pine adjoins Interior Douglas-Fir (Type 210) and Limber Pine (Type 219). In the East Humboldt, Ruby, Jarbidge, and Bull Run Ranges of northeastern Nevada, whitebark's principal associate is limber pine *(23)*.

In the timberline zone, conditions for tree development are so severe that any species that can become well established is considered a part of the climax community. In Montana and northern Idaho, the whitebark pine stands in the timberline zone (above forest line or where subalpine fir becomes stunted) make up the *Pinus albicaulis–Abies lasiocarpa* habitat types *(24,66)*. Whitebark pine is also a climax species in other habitat types, mostly on dry sites, in Montana, central Idaho, and western Wyoming *(71,72,83)*. *Pinus albicaulis/Vaccinium scoparium* is probably the most widespread and abundant habitat type that includes pure whitebark pine stands in the Rocky Mountains. Various aspects of the ecology of this habitat type in Montana and Wyoming have been described *(26,27,83)*.

In the subalpine forest of the Northern Rockies whitebark pine is a principal long-lived seral component of the *Abies lasiocarpa/Luzula hitchcockii* and *Abies lasiocarpa–Pinus albicaulis/Vaccinium scoparium* habitat types *(66)*. Prior to the early 1900's, whitebark pine was apparently more abundant in the subalpine forest as a result of natural fires, which favored its survival and regeneration over competing fir and spruce *(6,46,63)*. In the southern Canadian Rockies and the inland mountains of southern British Columbia, whitebark pine is also primarily a seral associate in the highest elevations of the subalpine fir-spruce forest *(1,9,65)*.

Principal undergrowth species in Rocky Mountain and northern Cascade stands include grouse whortleberry *(Vaccinium scoparium)*, mountain arnica *(Arnica latifolia)*, red mountain heath *(Phyllodoce empetriformis)*, rustyleaf menziesia *(Menziesia ferruginea)*, smooth woodrush *(Luzula hitchcockii)*, beargrass *(Xerophyllum tenax)*, elk sedge *(Carex geyeri)*, Parry rush *(Juncus parryi)*, Ross sedge *(Carex rossii)*, and Idaho fescue *(Festuca idahoensis)*. In south-central Oregon the primary undergrowth species are long-stolon sedge *(Carex pensylvanica)* and Wheeler bluegrass *(Poa nervosa)* (*41*). Undergrowth is sparse in Sierra Nevada stands.

Life History

Reproduction and Early Growth

Flowering and fruiting—Whitebark pine is monoecious. The female strobili and cones develop near the tip of upper crown branches while the male or pollen strobili develop throughout the crown on the current year's growth (*10,60*). Whitebark pine flowers are receptive and pollen is shed during the first half of July, but at some mid-elevation sites the species probably flowers in June. The ripe pollen strobili are a distinct carmine, which distinguishes them from the yellow pollen strobili of limber pine. The importance of various factors limiting pollination and fertilization is unknown. The isolation of some individual trees and small populations planted by birds, such as Clark's nutcracker, may prevent pollination. Also, animal planting of genetically similar seeds in a given area might increase the level of inbreeding, which might reduce regeneration success.

The female or seed cones ripen by early September of the second year (*81*). Although there are no good exterior signs of cone and seed ripeness, the cone scales open slightly—but not enough to release the seeds—and can be pulled apart after September 1.

Seed Production and Dissemination—Large seed crops are produced at irregular intervals, with smaller crops and crop failures in between. Cone crops may be produced more frequently in the southern parts of whitebark pine's distribution (*10*). In a Sierra Nevada study area, whitebark pine cone crops were moderate to heavy in each of four years, 1973 to 1976 (*74*). A study of 29 whitebark pine stands in the northern Rockies found that cone production averaged about 14,000 per hectare (6,000 per acre) over an 8-year period (*84*). Seeds number from 4,850 to 9,900/kg (2,200 to 4,500/lb) (*60,81*).

The large, heavy, wingless seeds are borne in dense, fleshy, egg-shaped cones usually 5 to 8 cm (2 to 3 in) long. The cone is dark purple, turning brown as it cures in late summer. It is unusual among cones of North American pines in remaining essentially closed (indehiscent) after ripening rather than spreading its scales to release seeds (*75*). Most of the cones are harvested by animals. Some fall to the ground where they disintegrate rapidly by decay and depredations by mammals and birds. A small percentage remain on the tree into winter. A few cones, complete with weathered scales but without seeds, remain on the branches for several years after ripening.

Clark's nutcrackers and red squirrels attack most of the ripening cone crop in the tree tops during August and September. As a result, it is common to find no evidence of cones in a whitebark pine stand except when a careful search is made for cone scales on the ground (*10*).

Clark's nutcrackers have an essential role in planting whitebark pine seeds (*42,49,51,74,76,77*). Nutcrackers can carry as many as 150 whitebark pine seeds in their sublingual (throat) pouch and they cache groups of one to several seeds in the soil at a depth of 2 to 3 cm (1 in), suitable for germination. Nutcrackers cached an estimated 33,600 limber pine seeds per hectare (13,600/acre) in one open, burned area during one summer; a similar pattern of seed caching would be expected for whitebark pine. Whitebark pine seeds sustain these birds and their young much of the year, but a large proportion of the seed caches go unrecovered.

The effects of whitebark pine seed planting by Clark's nutcrackers are readily observable. Despite its heavy wingless seed, this species often regenerates promptly on burned or clearcut areas where a seed source is absent (*46,59,76,77,78*). Moreover, whitebark pine seedlings in open areas frequently arise together in tight clumps of two to five. The species has become established atop a young geologic formation—Wizard Island in Crater Lake, Oregon, (*43*)—where seed dispersal by birds would have been necessary. Lone whitebark pine trees grow along alpine ridges, often several miles from the nearest possible seed source (*7*). Numerous clumped whitebark pine seedlings and saplings can be found far from a seed source in lower elevation forests (for example with ponderosa pine), where whitebark pine does not develop beyond sapling stage. Clark's nutcrackers migrate down to these stands in autumn, bringing whitebark pine seeds with them (*7,74*).

Various mammals also transport and cache whitebark pine seeds (*42,74*). Red squirrels harvest large quantities of whitebark pine cones and store them in rotten logs and on the ground. Black and grizzly bears raid many of these cone caches, scattering many seeds. Chipmunks, golden-mantled ground squirrels, and deer mice eat loose seeds and also cache seeds that may ultimately germinate. Red squirrels also cache whitebark pine seeds; from 3 to 176 seeds per cache have been found *(47)*.

A few seeds probably fall onto favorable seedbeds near the parent trees. Rarely, seeds may be carried by snow avalanches into lower elevations. Because of periodic disturbances and cold air drainage in avalanche chutes, whitebark pine saplings often occupy these sites at low elevations. Presumably, most of these trees arise from nutcracker caches.

The poor germination rate (8 to 14 percent) of whitebark pine seed under field conditions is apparently related to the development and condition of the embryo and to seed coat factors *(60)*. Seeds from three Canadian sources germinated poorly, despite a variety of seed coat scarification techniques with and without cold stratification *(68)*. The best results were obtained when a small cut was made in the heavy seed coat and the seed was placed adjacent to germination paper to facilitate water uptake. The seed coat is evidently a major cause of delayed regeneration or seed dormancy. Another factor explaining the low germination was the low proportion of seeds with fully developed embryos. In another test, using seed collected from Idaho, 61 percent of the seed germinated after clipping of the seed coat *(67)*. Stratification for 60 days plus clipping resulted in 91 percent germination. Cold stratification for at least 150 days followed by cracking of the seed coat has been fairly successful, resulting in 34 percent germination *(37)*.

Seedling Development—Germination is epigeal *(81)*. The newly germinated seedlings of whitebark pine are large compared with other mountain conifers. Cotyledons number 7 to 9 *(36)*, and while still in the cotyledon stage, the seedlings are 8 to 10 cm (3 to 4 in) tall, with a 13 to 18 cm (5 to 7 in) taproot *(25)*.

Vegetative Reproduction—Unlike associated subalpine fir, Engelmann spruce, and mountain hemlock, whitebark pine spreads only to a minor extent through layering—rooting of lower branches that are pressed against moist ground. At the upper elevational limit of tree growth, whitebark pine forms islands of shrub-like growth (flagged krummholz and cushion krummholz, fig. 2), similar in general appearance to the layered krummholz of fir and spruce described by Marr *(55)*. A recent inspection of whitebark pine krummholz in the Montana Bitterroot Range confirmed that layering occurs *(5)*. Investigation revealed that much of the spread of an individual krummholz plant results from branches extending horizontally from a central point, but also that in some plants these long branches become pressed into the surface soil and have developed large roots, which clearly constitutes layering.

Whitebark pine is easily grafted on rootstock of either whitebark pine or western white pine. The grafts grow much faster when the stock plant is western white pine *(44)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Whitebark pine is a slow-growing, long-lived tree. It can attain small to moderately large size after 250 or more years depending on site conditions. Growth and yield information on this species is scarce because it is of little interest for commercial timber production. Occasionally, old growth whitebark pine makes up a modest proportion of the timber harvested on moist, high-elevation sites.

In Montana, the best sites for whitebark pine timber growth are generally in the *Abies lasiocarpa/Luzula hitchcockii* habitat type, *Menziesia ferruginea* phase *(66)*. Although whitebark pines of good form and moderately large size [dominant trees 50 to 75 cm (20 to 30 in) in d.b.h. and 21 to 30 m (70 to 100 ft) tall at 250 to 300 years of age] sometimes develop on these sites, associated Engelmann spruce grows larger and is the primary object of management. In some commercial forest sites between 1520 and 1830 m (5,000 and 6,000 ft) in southwestern Alberta, whitebark pine grows larger than associated lodgepole pine and spruce *(25)*. In south-central Oregon, annual yields of merchantable timber in a lodgepole pine–whitebark pine type were estimated to be about 2.0 m^3/ha (29 ft^3/acre) *(41)*.

On the best sites, where whitebark pine is a component of the spruce–subalpine fir forest, it produces timber of good quality with only a moderate amount of defect. The resulting lumber has properties similar to those of western white pine *(45)* but is graded lower largely because of its slightly darker appearance *(85)*.

At higher elevations where the species is abundant, it forms a short tree with large branches and is unsuitable for timber production. Detailed information on productivity in some of the pure, high-elevation whitebark pine stands—Pinus albicaulis/Vaccinium scoparium habitat type—suggests that annual yields of merchantable timber are low, about 0.7 to 1.4 m^3/ha (10 to 20 ft^3/acre) *(27,83,66)*.

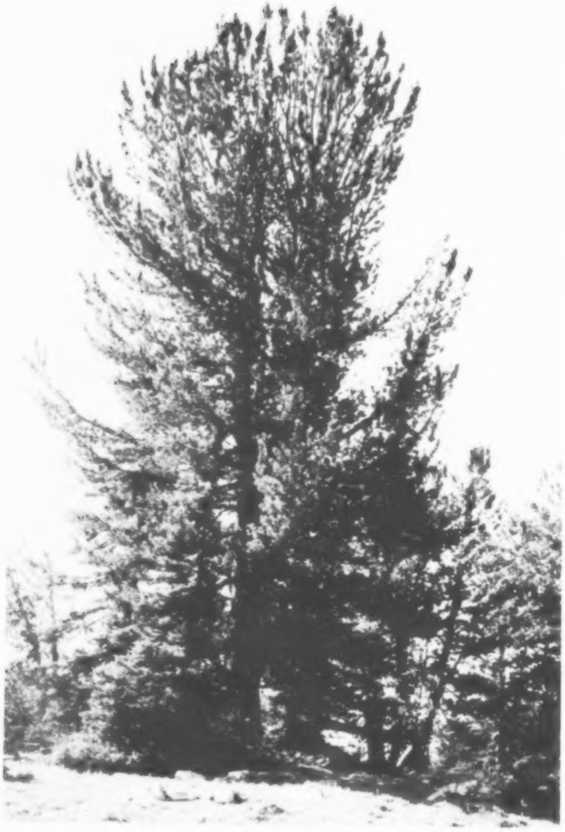

Figure 2—*Whitebark pine near timberline with typical upswept, branched crown.*

On favorable sites near the forest line, this species develops into a large, single-trunk tree commonly 11 to 20 m (35 to 65 ft) tall and has a life span of 500 years or more. The oldest individuals on some cold, dry sites probably attain 1,000 years. The ancient trees often have a broad crown composed of large ascending branch-trunks (fig. 3). The largest recorded whitebark pine, growing in central Idaho's Sawtooth Range, is 267 cm (8 ft 9 in) in d.b.h. and 21 m (69 ft) tall *(2)*. Upwards through the timberline zone, whitebark pine becomes progressively shorter and assumes multi-stemmed growth forms (fig. 4), evidently arising from the germination of nutcracker seed caches *(30,52)*. Because seeds in these caches often come from the same tree, the individual trees that make up a single multi-stemmed tree are often siblings. As a result, tree "clumps" may be composed of individuals more closely related to one another than to adjacent clumps.

At its upper limits, whitebark pine is reduced to shrublike growth forms (fig. 2) *(20)*. Such krummholz stands are often extensive on wind-exposed slopes and ridgetops. Primary causes of krummholz are thought to be inadequate growing season warmth, which prevents adequate growth, maturation, and hardening (cuticle development) of new shoots *(79)*. As a result, shoots are easily killed by frost or by heating and desiccation on warm sunny days in early spring when the soil and woody stems are frozen and thus little water is available to replace transpiration losses. Mechanical damage from ice particles in the wind is also a factor limiting krummholz growth to microsites where snowpack accumulates and provides protection from sun and wind.

Rooting Habit—On most sites, whitebark pine develops a deep and spreading root system. It is well anchored into the rocky substrate and is seldom uprooted despite its large, exposed crown and the violent winds to which it is subjected. Lanner *(50)*, however, observed shallow rooting that allowed windthrow in whitebark pines growing on moraines in Wyoming. These trees had pancake like root systems only 40 cm (16 in) deep. Shallow rooting probably occurs also where the species inhabits high-elevation bogs.

Reaction to Competition—Although whitebark pine has been tentatively rated very intolerant of competition or shade *(12)*, recent observers *(8,25,60,66,71)* believe that it is intermediate or intolerant, about equivalent to western white pine or interior Douglas-fir. Whitebark pine is less tolerant than subalpine fir, spruce, and mountain hemlock; however, it is more tolerant than lodgepole pine and alpine larch. In moist, wind-sheltered sites where spruce, fir, or hemlock are capable of forming a closed stand, whitebark pine can become a long-lived seral dominant in the aftermath of fires, snow avalanches, or blowdowns.

On a broad range of dry, wind-exposed sites, whitebark pine is a climax or near-climax species that persists indefinitely in association with subalpine fir and other tolerant species because it is hardier, more drought tolerant, more durable, and longer-lived. Even on these severe sites, however, a successional trend may be observable on a small scale: whitebark pine pioneers on an open site and is later surrounded and locally replaced by tolerant fir and hemlock *(29)*. In dry areas of Wyoming's Wind River and in south-central Oregon, whitebark pine forms a co-climax with lodgepole pine in dense subalpine forest stands *(41,72)*.

Observations of whitebark pine natural regeneration suggest that this species could be perpetuated on dry sites under a variety of even-aged or uneven-

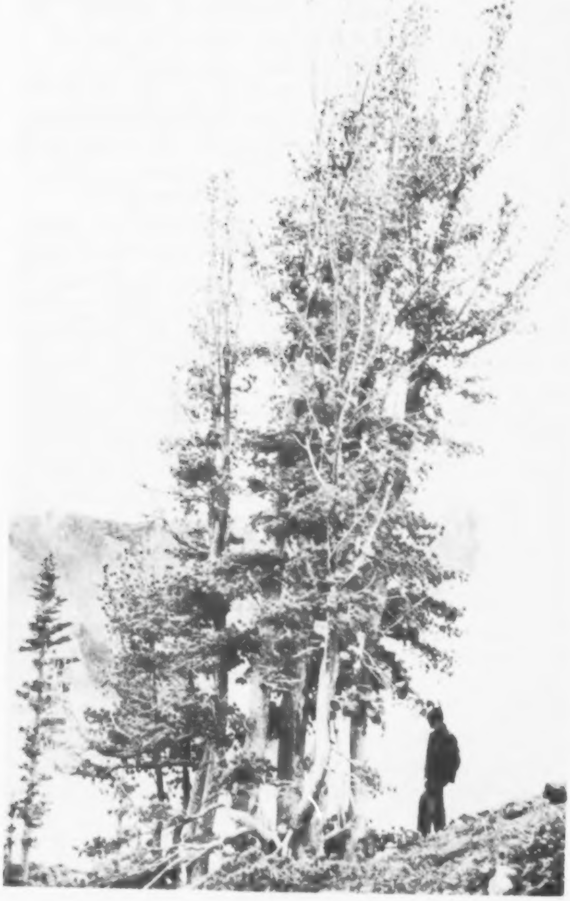

Figure 3—*Multi-stemmed growth form of whitebark pine at treeline in northeastern Olympic Mountains, WA.*

aged silvicultural systems. To establish whitebark pine on moist sites, some stand opening and light, localized site preparation are probably necessary. Wind-throw and wind breakage are a danger to residual trees, especially spruce and fir, in partial cuttings. Watershed values (and often esthetic values) are high on whitebark pine sites, however, and use of heavy equipment could be damaging. Whitebark pine can be regenerated by outplanting seedlings, or sowing seeds in mineral soil or at the soil-litter interface *(60)*.

Damaging Agents—Mountain pine beetle *(Dendroctonus ponderosae)* is by far the most damaging insect in mature stands of whitebark pine *(13)*. Much of the mature whitebark pine in the northern Rockies was killed by this insect between 1909 and 1940 *(3,19,31)*. Epidemics evidently spread upward into the whitebark pine forest after becoming established in the lodgepole pine forests below. In the 1970's, an epidemic developing in lodgepole pine in the Flathead National Forest of Montana killed most of the whitebark pine in some areas. This insect usually kills only the larger whitebark pine trees because such trees have an inner bark layer thick enough for the larvae to inhabit. Small trees are also killed in areas of intense infestation.

Less damaging insect infestations are caused by aphids *(Essigella gillettei)* that feed on needles, mealybugs *(Puto cupressi* and *P. pricei)* that feed on trunks and branches, and the lodgepole needletier *(Argyrotaenia tabulana)*, a potentially destructive defoliator. At least one species of Ips, the Monterey pine Ips *(Ips mexicanus)*, infests the bole, and *Pityogenes carinulatus* and *P. fossifrons* also infest the bole *(31)*. Two species of *Pityophthorus (P. aquilonius* and *P. collinus)* have been collected from whitebark pine *(18)*. The ponderosa pine cone beetle *(Conophthorus ponderosae)* infests cones of whitebark pine *(86)*.

The principal disease is the introduced white pine blister rust (caused by *Cronartium ribicola) (38)*. Blister rust is particularly destructive where the ranges of whitebark pine and blister rust coincide with good conditions for infection. This occurs where adequate moisture permits infection of local *Ribes* spp. (currant and gooseberry bushes, the rust's alternate hosts) in early summer and prevents drying of the infected *Ribes* leaves throughout the summer. Where there is a source of inoculum from lowland forests, the spores that infect pine can be carried by wind to the trees, but cool, moist conditions are needed for infection *(14)*. Blister rust damage is severe and prevents tree development in some timberline areas of the northern Cascades, northern Idaho, and northwestern Montana where whitebark pine is the major pioneer species *(48)*. (Resistance is discussed under "genetics".)

Several other diseases infect whitebark pine, generally with minor consequences *(34,35,69)*. These diseases are stem infections that produce cankers (some similar to blister rust), such as *Atropellis pinicola, A. piniphila, Lachnellula pini (Dasyscypha pini),* and *Gremmeniella abietina;* a wood rot organism *Phellinus pini;* several root and butt rots caused by *Heterobasidion annosum, Phaeolus schweinitzii,* and *Poria subacida;* and several needle

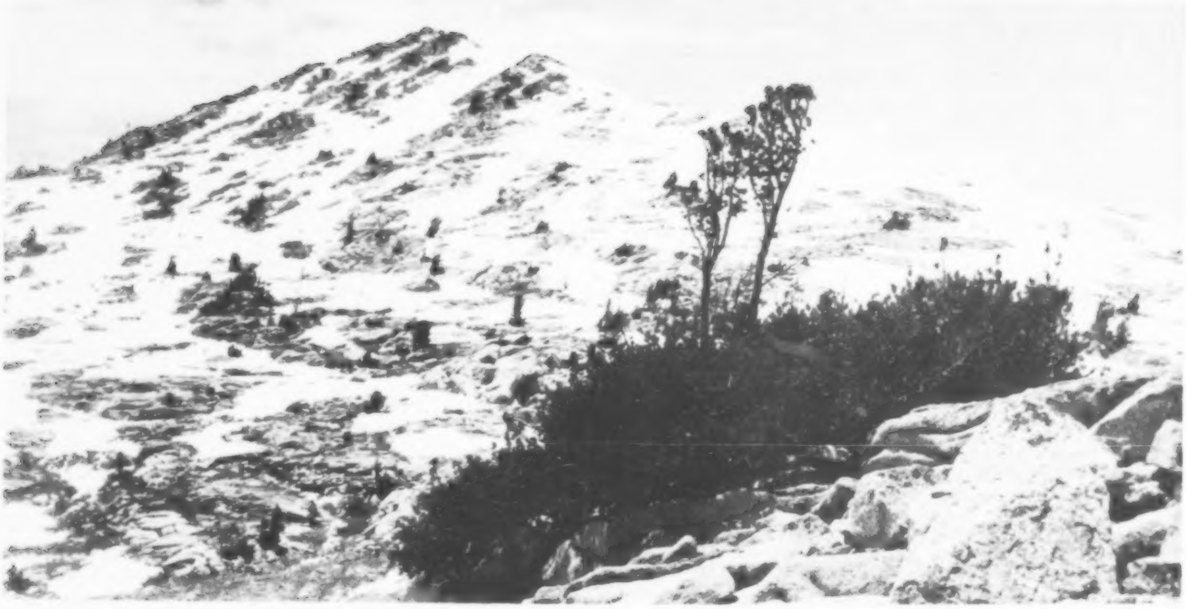

Figure 4—*Krummholz whitebark pine at 3230 m (10,600 ft) Granite Pass, Sequoia-Kings Canyon National Park, CA. The krummholz "cushion" is protected by winter snowpack; the wind-battered upper branches are called "flags."*

cast fungi including *Lophodermium nitens*, *L. pinastri*, *Bifusella linearis*, and *B. saccata*. When foliage is covered by snow for long periods, a snow mold, *Neopeckia coulteri*, appears *(34,35,69)*.

The dwarf mistletoes *(Arceuthobium* spp.) cause severe local mortality. The most widespread species is the limber pine dwarf mistletoe *(A. cyanocarpum)*, which causes extensive damage to whitebark pine on Mount Shasta and some nearby areas of northern California *(56)*. In the northern Rockies, the lodgepole pine dwarf mistletoe *(A. americanum)* occasionally occurs on whitebark pine where this tree grows in infested lodgepole pine stands. In the Oregon Cascades, the hemlock dwarf mistletoe *(A. tsugense)* is damaging to whitebark pine *(33,56)*.

In addition to these parasitic organisms, several harmless saprophytes grow on whitebark pine: *Lachnellula pini (Dasyscypha agassizii)* on dead bark and cankers of blister rust, *D. arida*, *Tympanis pinastri*, and *Phoma harknessii* on twigs *(34)*. *Cenococcum graniforme* has been identified as an ectotrophic mycorrhizal fungus of whitebark pine *(80)*.

Wildfire is an important vegetation recycling force in whitebark pine stands, although long intervals (50 to 300 years or more depending on the site) usually occur between fires in a given grove *(4)*. Lightning has been the major cause of fires in most stands; however, increased recreational use of forests results in accidental fires. Many of the fires have spread upslope into whitebark pine after developing in lower forests. Tiny spot fires are most common because fuels are generally sparse and conditions moist and cool. Nevertheless, occasional warm and dry periods accompanied by strong winds allow fires to spread. Spreading fires often remain on the surface and kill few large trees, but, under extreme conditions, severe wind-driven fires burn large stands *(4)*. Wildfire (enhanced by fuels created by epidemics of *Dendroctonus ponderosae* in lodgepole and whitebark pine), followed by seed dissemination by Clark's nutcrackers, may be the principal means by which whitebark pine becomes established in the more productive sites near its lower elevational limits. Conversely, after a severe fire on dry, wind-exposed sites, regeneration of whitebark pine (often the pioneer species) may require several decades *(6,77)*.

Wind breakage of the crowns or boles occurs when unusually heavy loads of wet snow or ice have accumulated on the foliage. This damage is prevalent in large, old trees having extensive heart rot. Snow avalanches also are an important damaging agent in some whitebark pine stands.

Special Uses

Whitebark pine's greatest values are for wildlife habitat, watershed protection, and esthetics. Seeds are an important, highly nutritious food source for many seed eating birds and small mammals, as well as for black bears and grizzly bears *(47,57,61)*.

Blue grouse feed and roost in whitebark pine crowns during much of the year. This tree provides both hiding and thermal cover in sites where few if any other trees grow. The large, hollow trunks of old trees and snags provide homesites for cavity-nesting birds. The seeds of whitebark pine were occasionally used as a secondary food source by Native Americans *(17,54)*.

Whitebark pine helps to stabilize snow, soil, and rocks on steep terrain and has potential for use in land-reclamation projects at high elevation *(68)*. It provides shelter and fuel for hikers and campers and is an important component of the picturesque setting that lures hundreds of thousands of visitors into the high mountains *(21)*.

Genetics

Most of the wide phenotypic growth form variation in whitebark pine is apparently the result of differences in site and climate. Krummholz whitebark pines have apparently arisen from nutcracker caches of seeds from erect trees *(77)*, implying that the prostrate form is environmentally induced. Conversely, Clausen *(20)* hypothesized that the alpine (krummholz) and subalpine (tree) forms have a genetic basis. Determination of this will have to await genetic tests. Enzyme studies suggest that high-elevation forms of Engelmann spruce and subalpine fir do have a genetic basis *(32)*, but another study showed that a prostrate form of the European stone pine *(Pinus cembra)*, closely related to whitebark, can spontaneously produce an erect tree stem *(40)*.

Resistance to white pine blister rust is the most notable phenotypic variation observed in whitebark pine. The species was extremely susceptible to blister rust both in the field and nursery in artificial inoculation tests and has been rated by many people as the most susceptible of all the world's white pines *(15)*. In stands where mortality has been as high as 90 percent, however, many individuals have survived and some are free of rust symptoms. Genetic testing, using artificial inoculation methods to expose seedlings from uninfected wild parents, has demonstrated resistance to be genetic *(38)*. Four main defense mechanisms were observed: absence of infections of needles or stem, shedding of infected needles before the fungus could reach the stem, a chemical interaction between the fungus and short-shoot tissue that killed the fungus, and chemical reactions in the stem that killed host cells, with subsequent walling off of the fungus.

A small trial plantation of first-generation wind-pollinated seedlings from resistant whitebark pine parents was established at Marks Butte near Clarkia, Idaho, in 1979 *(37)*. A survey in 1989 revealed 10 surviving seedlings of 200 planted. The survivors were about 1 foot tall. Much of the mortality was due to vegetative competition, especially by beargrass. Survival of planted resistant seedlings would provide a first step toward returning whitebark pine as an important component of the subalpine plant communities, where the adverse impact of birds and rodents on the rust-induced mortality is high and where remaining seed supply is great.

Many attempts have been made to cross whitebark pine with the other four white pine species in its subsection *Cembrae* and with most species in subsection *Strobi*. Almost all have ended in failure or inconclusive results *(16)*. Only the cross with limber pine, from subsection *Strobi*, offers slight hope *(22)*. No putative hybrids of whitebark pine have been identified in natural stands.

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Pinus banksiana Lamb. Jack Pine

Pinaceae Pine family

T. D. Rudolph and P. R. Laidly

Jack pine *(Pinus banksiana)*, also called scrub pine, Banksian pine, or Hudson Bay pine, is a small-to medium-sized coniferous tree of the northern forests of the United States and Canada, where it is an important source of pulpwood, lumber, and round timber *(1,10,15,16)*. It grows farther north than any other American pine and is the most widely distributed pine species in Canada. It is a pioneer species in succession and invades areas where mineral soil has been exposed by major disturbances such as fires. It usually grows in even-aged pure or mixed stands on less fertile and drier soils than those required by other native species in its range *(38)*.

Habitat

Native Range

The major portion of the jack pine range (fig. 1) is in Canada where its northern boundary extends eastward from the Mackenzie River in the Northwest Territories across the country to Cape Breton Island, NS. The range then extends southwest through Maine, New Hampshire, northern New York, central Quebec and northern Ontario, Michigan, extreme northwest Indiana, northeast Illinois, then northwest through Wisconsin, Minnesota, Manitoba, Saskatchewan, central Alberta, to extreme northeast British Columbia *(72)*.

Within its range, jack pine is widely but not continuously distributed. In Canada it is most abundant in Ontario, and in the United States, the largest acreages are in Minnesota, Wisconsin, and Michigan *(74)*. The only significant artificial extensions of the jack pine range have been on strip-mined areas in the central and northeastern States *(61)* and on the sand hills of Nebraska *(11)*.

Climate

In the eastern part of its range, jack pine grows in a maritime climate but elsewhere it is found in diverse continental climates characterized by short, warm to cool summers, very cold winters, and low rainfall. The average January and July temperatures range from -29° to -4° C (-20° to 25° F) and from 13° to 22° C (55° to 72° F), respectively. Average annual maximum temperatures range from 29° to 38° C (85° to 100° F), and average annual minimum temperatures are from -21° to -46° C (-5° to -50° F) *(61)*. Mean annual temperatures range between -5° and 4° C (23° and 40° F) *(74)*. The northern limits of the range closely parallel the 29° C (85° F) mean annual maximum isotherm. Frost may occur in some areas during any month and in the Northwest the range extends into the permafrost zone. *(61)*.

Average annual precipitation ranges from 250 to 1400 mm (10 to 55 in) but 380 to 890 mm (15 to 35 in) are more usual. The average warm season precipitation ranges from 150 to 640 mm (6 to 25 in). Annual snowfall is from 76 to 508 cm (30 to 200 in), but over much of the range it is between 102 and 254 cm (40 to 100 in). Summer droughts are common in the south-central and western portions of the range *(61)*.

The average date of the last killing spring frost ranges from April 30 to about July 1; and the average date of the first killing fall frost ranges from about August 10 to October 20. The frost-free period averages from 50 to 173 days but is usually from 80 to 120 days. Generally, temperature, rainfall, and frost-free period increase from the northwestern toward the southeastern part of the range *(61)*.

Soils and Topography

Jack pine is usually found on sandy soils of the Spodosol and Entisol soil orders *(81)*. It also grows on loamy soils, on thin soils over the granites and metamorphosed rocks of the Canadian Shield, over limestones, on peats, and on soil over permafrost *(16,61,74)*.

Jack pine can grow on very dry sandy or gravelly soils where other species can scarcely survive, but it grows best on well drained loamy sands where the midsummer water table is from 1.2 to 1.8 m (4 to 6 ft) below the surface. Jack pine does not grow naturally where the surface soil is alkaline, but it does grow on soils overlying limestone. It can grow on calcareous soils (pH 8.2) if a normal mycorrhizal association is present. In southeastern New Brunswick, owing to a long fire history, jack pine occupies vast areas of clayey soils and it is more common than red pine on xeric sites that have high nutrient levels *(61)*.

In well stocked stands in Minnesota and central Wisconsin, available moisture-holding capacity in the

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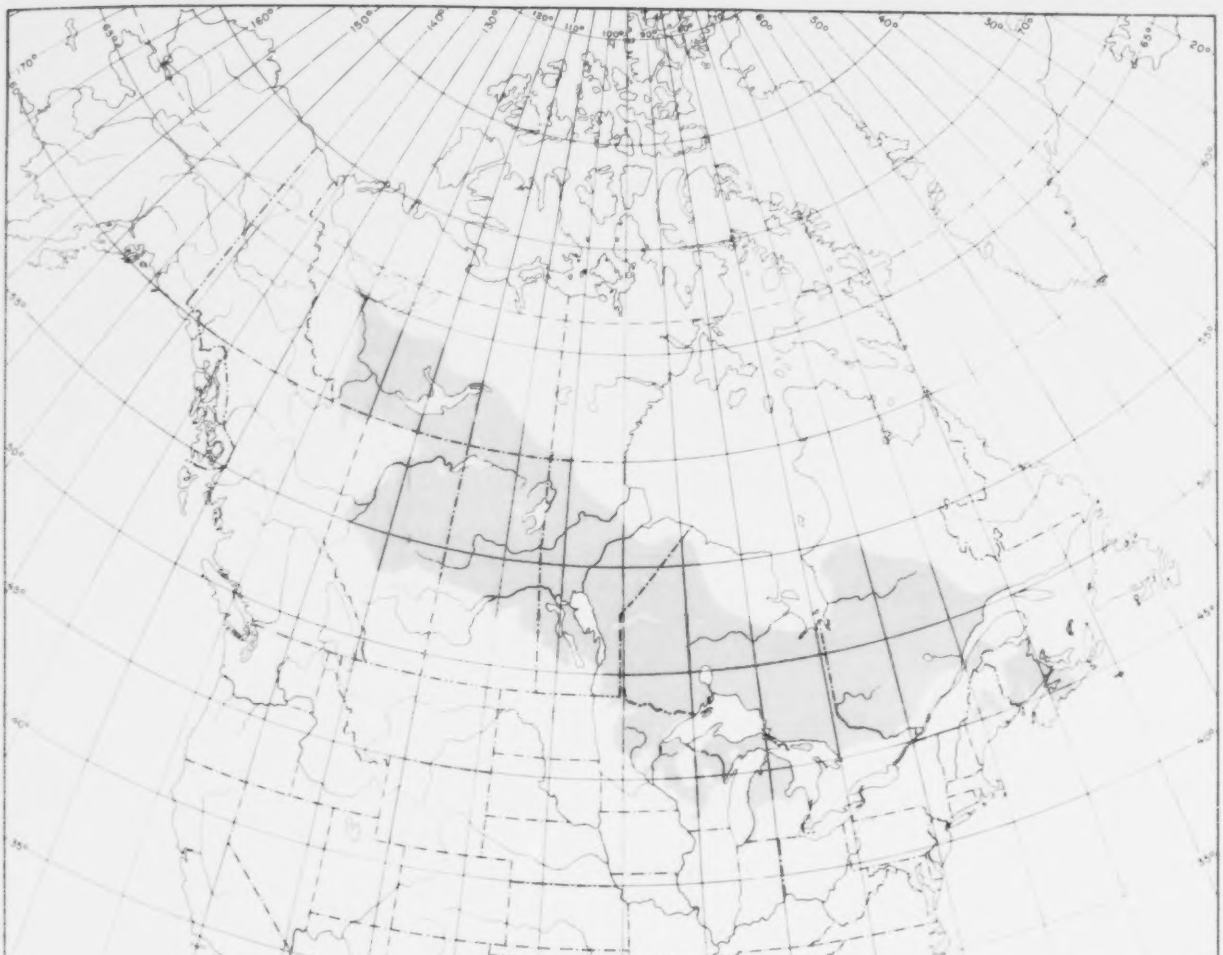
1984
120°
115°
110°
105°
100°
95°
90°
85°
80°
75°
70°

Figure 1 — *The native range of jack pine.*

best copy available

upper 30 cm (12 in) ranges from 3 to 17 percent by weight. Site index improves with an increase in fine sand and silt and clay in the upper soil layer, an increase in water-holding capacity (up to a point after which it levels off), and an increase in cation exchange capacity in the A and B horizons *(61)*. Similar relations between these soil factors and site index were found for plantations in Wisconsin *(82)*.

In a jack pine forest in northeastern Minnesota about 2580 to 3140 kg/ha (2,300 to 2,800 lb/acre) ovendry weight of organic matter was returned to the soil annually. The quantity of nutrient elements, expressed in percentage of dry weight, in freshly fallen jack pine litter averages as follows: calcium, 0.61; potassium, 0.16; phosphorus, 0.04; nitrogen, 0.58; and ash, 4.15. The litter is acid with a pH of 3.8 to 4.3 *(61)*. Accumulated biomass of vegetation in jack pine stands more than 50 years old in northeastern Minnesota was 89 000 kg/ha (79,400 lb/acre) on shallow soils over bedrock, and 152 800 kg/ha (136,300 lb/acre) on deep till soils. Biomass of the forest floor was 35 200 kg/ha (31,400 lb/acre) on shallow soils and 50 300 kg/ha (44,870 lb/acre) on deep till soils. Nutrients in the vegetation, forest floor, and soil were similarly higher on the deep till soils *(33)*. The above values largely agree with those found on other sites for jack pine forest floor biomass, litter fall, and nutrient transfer from jack pine forest to soil *(28,49,78)*.

In the Lake States and Canada, jack pine grows most commonly on level to gently rolling sand plains, usually of glacial outwash, fluvial, or lacustrine origin. It occurs less commonly on eskers, sand dunes, rock outcrops, and bald rock ridges. In the Lake States jack pine is found chiefly at elevations between 300 and 460 m (1,000 and 1,500 ft), with a maximum of about 610 m (2,000 ft) above sea level. In the East, jack pine grows on a variety of sandy sites from near sea level up to about 610 m (2,000 ft), with an outlier in New Hampshire at 760 m (2,500 ft) *(61)*.

Associated Forest Cover

The Jack Pine forest cover type (Society of American Foresters Type 1) *(26)* typically originates after forest fires. It is found in pure, even-aged stands or as a majority of the stocking over vast areas of Canada and to a much lesser extent in the Lake States and the northeastern United States *(61)*. In the boreal forest jack pine is also a component of three other forest cover types–Black Spruce (Type 12), Paper Birch (Type 18), and Aspen (Type 16). In the northern forest region it is a component of two forest cover types—Red Pine (Type 15) and Northern Pin Oak (Type 14). Outliers near southern fringes of the species' range are found in various types of hardwood forest *(12)*.

Associated tree species, listed in order of presence on dry to mesic sites, include northern pin oak *(Quercus ellipsoidalis)*, bur oak *(Q. macrocarpa)*, red pine *(Pinus resinosa)*, bigtooth aspen *(Populus grandidentata)*, quaking aspen *(P. tremuloides)*, paper birch *(Betula papyrifera)*, northern red oak *(Quercus rubra)*, eastern white pine *(Pinus strobus)*, red maple *(Acer rubrum)*, balsam fir *(Abies balsamea)*, white spruce *(Picea glauca)*, black spruce *(P. mariana)*, tamarack *(Larix laricina)*, and balsam poplar *(Populus balsamifera)*. In the boreal forest the most common associates are quaking aspen, paper birch, balsam fir, and black spruce. In the northern forest they are northern pin oak, red pine, quaking aspen, paper birch, and balsam fir. Associates are nearly always subordinate to jack pine except for aspen, paper birch, and red pine which may be coordinate *(26,61)*. Infrequent associates in the northeastern United States and adjacent Canada include white oak *(Quercus alba)*, pin cherry *(Prunus pensylvanica)*, gray birch *(Betula populifolia)*, red spruce *(Picea rubens)*, and pitch pine *(Pinus rigida)* *(61)*.

In Canada, six subtypes of jack pine may be recognized based upon the edaphic and climatic conditions where they are found and on associated species as follows: jack pine–balsam fir–black spruce (subtype a); jack pine–feather moss (subtype b); jack pine–sheep laurel (subtype c); jack pine–sphagnum (subtype d); jack pine–labrador-tea (subtype e); jack pine–lichen (subtype f) *(26)*.

The preceding subtype descriptions apply primarily to eastern Canada. However, jack pine forests in Saskatchewan bear close resemblance to some of the subtypes described above *(43)*.

Subtypes, as such, are not recognized in the Lake States. There are, however, certain variants of the type, including jack pine–black spruce, jack pine–red pine, and northern pin oak–jack pine *(26)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Jack pine is a monoecious species. Ovulate cones are usually borne on primary and secondary branches in the upper tree crown and staminate cones are usually borne on tertiary branches lower in the crown. Ovulate cones are modified long shoots and staminate cones are modifed dwarf shoots *(24)*.

In northeastern Wisconsin, bud initiation for the following year's shoot systems begins in late June or early July. Staminate cone primordia are initiated in early or mid-July but ovulate primordia are not initiated until August. By early September the staminate cone primordia are about 1 mm (0.04 in) long and remain that size until spring. Then they elongate to about 5 mm (0.2 in) by the middle of May and early June just before pollen is shed. Rapid elongation up to several more millimeters occurs as the pollen is shed. Time of pollen shedding (anthesis) varies greatly from year to year depending on the weather *(23)*.

Fertilization occurs about 13 months after pollination when the female cone is approaching its maximum size *(27)*. Jack pine is normally a wind-pollinated, cross-fertilizing species but up to 25 percent or rarely more natural selfing can occur *(29,64)*. Under natural conditions, however, survival of selfed and other inbred seedlings is severely reduced by natural selection against the semilethal and other deleterious characteristics carried by the inbred seedlings *(67)*.

Cones mature and the seeds ripen late in the growing season of the year after pollination. Various cone and seed characteristics, including cone color, volume, fresh and dry weight, specific gravity, scale color, seed color, and embryo length, can aid in determining seed ripeness. In northeastern Wisconsin the best indicators of cone and seed ripeness are cone color, 75 percent brown; insides of the cone scales, reddish brown; seeds, dark brown or black; and cone moisture content, less than 45 percent of fresh weight. These indicators of cone and seed ripeness coincide with the beginning of cone harvesting by squirrels about September 10. Because specific gravity of the serotinous cones usually remains above 1.0 at least until February, flotation techniques cannot be used to evaluate cone and seed ripeness in jack pine *(18)*.

Seed Production and Dissemination—Jack pine trees, particularly under good early growing conditions, begin to flower at a younger age than most other pine species *(41,65,68)*. Under near optimum growing conditions in the greenhouse and nursery, female flowering can be induced in a small percentage of seedlings as early as 12 months from seed sowing *(68)*. Male flowering under these conditions usually does not begin until the fourth year. An accumulated yield of 2,861,000 filled seeds per hectare (1,158,000/acre) can be produced through the first 8 years in plantations with 2.4 m (8 ft) between trees *(67)*.

In naturally regenerated stands, jack pine typically begins to flower at 5 to 10 years under open-grown conditions but not until later in closed stands *(61)*. Once cone production in jack pine begins, it is fairly regular and increases until crown competition becomes a factor. Seed production differs from year to year but some seed is usually produced every year and total crop failures are rare *(31,61)*.

Seed yields per cone range from about 15 to 75 *(72)*. Strongly curved cones yield less seed than straight ones *(72)*. Ovulate abortion on the inner curvature of cones is twice that on the outer curvature *(17)*. The average number of scales per cone can be more than 80 but usually only a little more than one-third of the scales, those in the upper end of the cones, bear seeds *(72)*.

Over much of its natural range jack pine bears predominantly serotinous cones, but in the southern part cones are nonserotinous. Total seeds stored on the trees in serotinous cones can reach more than 14.6 kg or 4 million seeds per hectare (13.0 lb or 1.6 million/acre) in well stocked mature stands *(61)*. As viability after 5 to 10 years may be significantly reduced, however, only cones 6 years old or less should be collected *(8)*. Commercially cleaned seeds range between 156,500 and 551,000/kg (71,000 and 250,000/lb) with an average of 288,800/kg (131,000/lb) *(45)*.

Well-stocked, mature stands in the Lake States dispersed an annual average of 6,670 to 25,950 seeds per hectare (2,700 to 10,500/acre) over 5 years; much of the total crop remained in the unopened cones. In areas with nonserotinous or partially serotinous cones, seed may be disseminated during any season. The effective range of seed dissemination, as measured by established seedlings, is about two tree heights although it is low beyond one tree height *(61)*.

The melting temperature of the resinous bonding material of the cone scales is 50° C (122° F), but it is likely that the bonding resin softens at lower temperatures in the nonserotinous types in the southern portion of the species' range. The mechanism of cone opening in both serotinous and nonserotinous cones is hygroscopic. Once the bonding material of the cone scales is broken, the quantity of water in the scales is the limiting factor in scale movement and flexing outward under drying condition *(35,61)*.

Jack pine cones open most readily during dry weather when the temperature is at least 27° C (80° F), although many of them remain closed until they are exposed to fire or high temperatures near the ground after wind breakage or logging. Over most of its range where serotinous cones are common, up to 50 percent may open on the sunny part of the crown. Cones may also open in very cold winters when the temperature is -46° C (- 50° F) or colder *(61)*.

Cone and seed crops in jack pine may be reduced by numerous agents *(61)*. Rainy weather at time of pollination may reduce seed set. Cone and seed production are also reduced by cone and ovulate abortion *(17,66)*, but the severe losses previously attributed to abortion may be partially the result of insect attacks. Within a cone, all the ovules near the base of the cone abort and abortion decreases toward the tip *(17)*.

Seedling Development—Germination is epigeal (45). Jack pine seed usually germinates within 15 to 60 days under favorable conditions *(61)*, but some seeds require more than 100 days to germinate *(72)*. Delayed germination of direct seeding increased stocking between the first and third year after sowing *(60)*.

Under forest conditions with adequate moisture, seeds germinate when air temperatures reach 18° C (64° F) but light also influences germination *(2,61)*. Under continuous light, germination was complete at a range of temperatures from 16° to 27° C (60° to 80° F) *(2)*. Germination was markedly reduced at all temperatures when light was excluded. The shade cast by slash and snags on burned-over or cut-over areas to reduce surface temperature and drying undoubtedly contributes substantially to the good germination often observed on such areas *(16)*.

Type of seedbed is an important factor affecting jack pine seed germination *(16,61)*. In northeastern Minnesota, germination under clearcut and partially cut jack pine stands averaged 60 percent on mineral soil, 49 percent on burned duff, 47 percent on scarified and shaded duff, and 17 percent on undisturbed duff *(61)*. The poor germination on litter and humus is caused by poor moisture conditions and it can be satisfactory in years of above normal precipitation. Germination may be delayed by spring drought *(16)*. Associated species can affect germination, survival, and growth of jack pine differentially, probably as a result of allelopathy *(13)*.

Survival on various seedbeds shows the same trend as germination *(61)*. Optimum conditions for jack pine seedling establishment and survival are provided by mineral soil and burned seedbeds where competition from other vegetation is not severe *(16)*, the water table is high, and there is some shade *(61)*. Competition from shrubs and herbaceous vegetation, together with smothering by fallen leaves, are important causes of seedling mortality on sandy soils in Ontario. On clay soils in Manitoba and Saskatchewan, competition from aspen and hazel are responsible for poor survival. On similar soils in western Manitoba competing grasses kill many seedlings *(16)*.

Most of the older jack pine stands appear to have been established following fires *(61)*. Although jack pine seed usually germinates following fire, most of the seedlings die unless the organic matter left on the soil is less than 1.3 cm (0.5 in) thick. Most germination occurs the first and second season following fire, with most mortality between the first and second growing season. Unless conditions for germination and early survival are favorable, good regeneration does not necessarily follow burns (20,61).

Young seedlings grow tallest in full sunlight *(48)*, although under stands their initial abundance may be greatest in light intensities of 11 to 30 percent of full sunlight, but no seedlings are found at 60 percent and higher crown cover *(61)*.

Under forest conditions, seedling growth is slow in the first 3 years but increases rapidly beginning in the fourth and fifth years. Seedlings attain a height of about 5 cm (2 in) the first year, 15 cm (6 in) at 2 years, and 30 to 90 cm (12 to 36 in) at 4 years. Early growth of 2-0 seedlings in plantations is more rapid, amounting to 30 to 45 cm (12 to 18 in) per year on medium sites *(61)*.

Shoot growth begins in late April and early May at Cloquet, MN, and Chalk River, ON *(62,63,80)*, and about May 10 in the Upper Peninsula of Michigan *(61)*. Essentially all height growth is completed in 61 to 68 days at the three locations. Maximum growth rate approaches 1 cm (0.4 in) per day in both Minnesota and Ontario. Although shoot growth in jack pine ceases long before the end of the frost-free season, the remaining time may be necessary to complete latewood growth, lignification, terminal bud development, and hardening off to resist frost *(80)*.

If favorable moisture conditions prevail in late summer, jack pine frequently has a second period of shoot elongation and produces lammas and proleptic shoots *(62,63)*. Trees with lammas shoots had a longer growth period than those without them but did not grow significantly less the following year. The late growth does not result in detectable increases in diameter growth and it may or may not result in false rings. Fall frost injury resulting in frost rings, however, may be frequent in the current shoots of trees with lammas growth.

Vegetative Reproduction—Under natural conditions jack pine does not reproduce vegetatively. Jack pine cuttings from young trees can be rooted but rooting ability decreases rapidly with increasing ortet age. Cuttings from 4-month-old seedlings gave 75 percent rooting *(7)* but average rooting was only 7 percent in cuttings from 6-year-old ortets and 5 percent in those from 10-year-old ortets *(90)*. Clonal variation in rooting percentage ranged from 0 to 31.

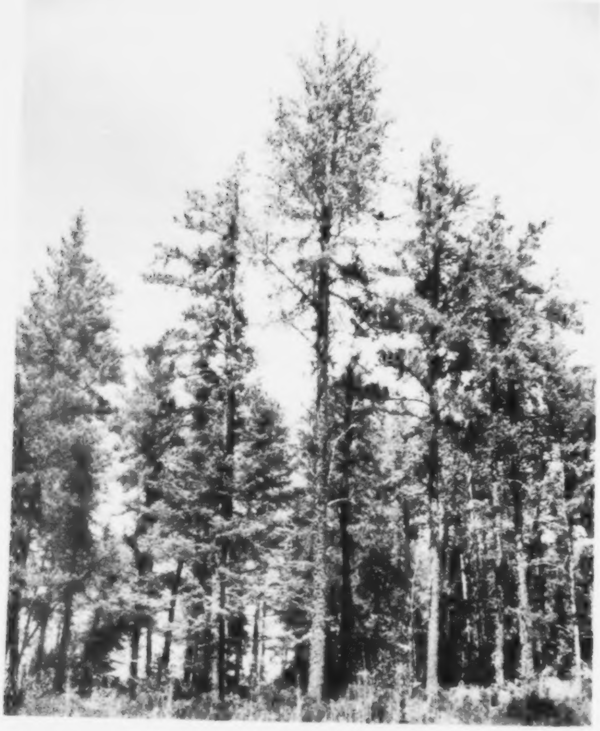

Figure 2 — *A stand of jack pine in Minnesota.*

Aryl esters of indole auxins can enhance rooting of jack pine cuttings taken from young seedlings. Phenyl indole-3-butyric (P–IBA) treatment caused 12 percent more jack pine cuttings to root than did treatment with indole-3-butyric acid (IBA), and up to 30 percent more than no treatment *(34)*.

Rooting needle fascicles has potential for establishing large clones in a short time. Shearing the terminal buds on trees up to 5 years old induces the fascicular buds to differentiate and develops shoots. Treating such shoots from 2-year-old trees with IBA (0.1 percent) and placing them in a heated rooting medium under a 20-hour photoperiod resulted in up to 70 percent rooting *(71)*.

Jack pine can be grafted, most successfully using dormant scions and when grafting is done just as the rootstock resumes growth in the spring. Both early and delayed graft incompatibility may occur; the causes are unknown *(72)*. No complete jack pine plants have yet been propagated from either callus tissue or cell suspension cultures *(72)*.

Sapling and Pole Stages to Maturity

In well-stocked stands, jack pine (fig. 2) develops into a short to medium-tall, slender tree with a narrow, open crown covering 30 to 45 percent of the stem *(61)*. Crown ratios from 10 to 20 percent are not uncommon in dense stands. Open-grown jack pine develops a stocky stem of poor form and a wide, spreading crown with persistent branches, often to the ground. Overstocked stands produce weak, spindly stems that are susceptible to breakage by wind, ice, and snow *(10)*.

Growth and Yield—During the first 20 years, jack pine in its native range is the fastest growing conifer other than tamarack *(61)*. Seedlings reach 1.4 m (4.5 ft) tall in 5 to 8 years, depending on site. In the Lake States, 20-year-old stands with 2,470 trees per hectare (1,000/acre) on sites ranging from site index 12 to 21 m (40 to 70 ft) average between 5.5 and 9.8 m (18 and 32 ft) tall, 6.7 and 20.0 m^2 (29 and 87 ft^2) in basal area, 5.8 and 10.2 cm (2.3 and 4.0 in) in d.b.h. *(46)*, and 14 600 and 62 800 kg/ha (13,000 and 56,000 lb/acre) in ovendry weight of aboveground biomass *(3)*.

The generalized equations used to derive these biomass estimates *(3)* give results similar to biomass production reported in other natural jack pine stands *(22,32,37,51)*. Mean annual biomass production of 43-year-old natural jack pine stands in Quebec ranged from 1.42 to 2.47 t/ha (0.63 to 1.10 tons/acre) *(28)*; in 7- to 57-year-old jack pine in New Brunswick from 0.94 to 2.76 t/ha (0.42 to 1.23 tons/acre) *(51)*; and in 20- to 100-year-old stands in Ontario from about 1.17 to 3.38 t/ha (0.52 to 1.51 tons/acre) *(45)*. In 24- and 25-year-old plantations in the Lake States, the highest mean annual biomass production was 58 percent higher than the maximum reported in the literature, when seed source and site were properly matched *(89)*.

Annual height growth on medium sites (site index 17 m (55 ft)) in the Lake States averages from 33 cm (13 in) at age 30 to 23 cm (9 in) at age 50. At age 80 years, annual height growth is only 13 cm (5 in) *(46)* On typical sand plains sites, growth is about one site quality better where the water table is 1.2 to 1.8 m (4 to 6 ft) from the soil surface than where it is deeper *(61)*.

Normally, mature trees are about 17 to 20 m (55 to 65 ft) tall and 20 to 25 cm (8 to 10 in) d.b.h., although some trees have attained 30 m (100 ft) in height and 64 cm (25 in) in d.b.h. *(46,61)*, and one tree listed by the American Forestry Association in 1982 measured 73.4 cm (28.9 in) in d.b.h. and 25.6 m (84 ft) tall. Stand basal areas seldom exceed 37 m^2/ha (160 ft^2/acre) *(46)*. Jack pine stands begin to disintegrate after 80 years on the best sites and after 60 years on the poorest sites. Vigorous trees 185 years old have been found in northwestern Minnesota, however. The oldest tree reported—230 years old—was found east of Lake Nipigon in Ontario *(61)*.

Growth is somewhat slower, but maintained longer, in Canada. Average stocking on sites having a site index range of 14 to 17 m (45 to 55 ft) in southern Manitoba produces a culmination of mean annual increment at 50 to 60 years with 1.6 to 3.2 m^3/ha (23 to 46 ft^3/acre) of merchantable material *(9)*. For average site (site index 14 m (45 ft)) and stocking in Saskatchewan, mean annual increment culminates at about 70 years with 2.0 merchantable m^3/ha (28 ft^3/acre) *(42)*. In fully stocked stands on average sites (site class 2) in Ontario, mean annual increment culminates at about age 60 with 2.7 m^3/ha (38 ft^3/acre) of merchantable material *(54)*.

Yields from well-stocked, unmanaged jack pine stands in the Lake States at 60 years are shown in table 1 *(46)*, along with yields from well-stocked unmanaged stands in Saskatchewan *(42)*. Rotation age of 40 to 50 years is recommended to produce pulpwood and 60 to 70 years is recommended to produce poles and sawtimber.

Rooting Habit—Jack pine frequently develops a taproot as a seedling and maintains it to maturity. During the first growing season under natural conditions the seedling root system penetrates to a depth of 13 to 25 cm (5 to 10 in). By the end of the second growing season jack pine seedlings on typical sandy soils in the open have a dry weight between 1 and 2 g (0.04 and 0.08 oz), have developed 8 to 10 cm (3 to 4 in) tops, and have root systems from 28 to 33 cm (11 to 13 in) deep and from 46 to 61 cm (18 to 24 in) wide. On a moist sandy soil with the water table about 76 cm (30 in) below the surface in Upper Michigan, roots penetrated to 53 cm (21 in) in 2 years but only to 61 cm (24 in) by 7 years; the lateral spread, however, increased from 0.9 to 1.2 m (3 to 4 ft) at 2 years to 4.3 to 4.9 m (14.0 to 16.2 ft) at 7 years. In the 7-year-old trees the average volume of the top, stem, branches, and foliage was about 4000 cm^3 (244 in^3) as compared to 1200 cm^3 (73 in^3) for the root system *(61)*.

In northern Minnesota, root growth begins when the temperature reaches 4° C (40° F) in the upper 15 cm (6 in) of soil, usually within a week of the onset of shoot growth. Root growth ceases in the fall when soil temperature drops to 7° C (45° F) for 6 days or more. In some years root growth may begin in April and continue to late October. Seven-year-old trees elongated their lateral roots an average of 38 cm (15

Table 1—Yields of unmanaged jack pine stands in the Lake States and in Saskatchewan by age and site index

Age	Height[1]	Basal area	Total volume	Merchantable volume
yr	*m*	*m^2/ha*	*m^3/ha*	*m^3/ha*
		Lake States		
Site index[2] 12.2 m				
30	8.2	12.2	41	31
40	10.4	15.8	67	52
50	12.2	18.4	92	71
60	13.7	20.4	114	88
Site index 18.3 m				
30	12.2	23.0	115	83
40	15.5	27.3	174	134
50	18.3	30.1	224	173
60	20.4	31.7	265	206
		Saskatchewan		
Site index 10.1 m				
30	5.8	11.7	45	10
40	8.2	14.0	66	34
50	10.1	15.8	85	56
60	11.9	17.0	102	75
Site index 17.4 m				
30	11.6	19.3	112	61
40	14.6	23.2	140	98
50	17.4	26.2	168	134
60	19.8	28.2	195	165
	ft	*ft^2/acre*	*ft^3/acre*	*ft^3/acre*
		Lake States		
Site index 40 ft				
30	27	53	580	448
40	34	69	956	736
50	40	80	1,311	1,008
60	45	89	1,631	1,264
Site index 60 ft				
30	40	100	1,647	1,272
40	51	119	2,484	1,920
50	60	131	3,194	2,472
60	67	138	3,789	2,936
		Saskatchewan		
Site index 33 ft				
30	19	51	645	150
40	27	61	940	485
50	33	69	1,210	800
60	39	74	1,460	1,070
Site index 57 ft				
30	38	84	1,600	865
40	48	101	2,000	1,403
50	57	114	2,405	1,910
60	65	123	2,785	2,360

[1] Mean height of dominants and codominants.

[2] Height of dominants and codominants at 50 years.

in) in 1 year *(61)*. In Manitoba, root development of jack pine growing on dry and fresh sands was confined mainly to the taproot for the first 1 to 3 years, but lateral branching became increasingly common on 3- to 4-year-old seedlings. Mycorrhizae were found on 1-year-old seedlings *(16)*.

On deep, well-drained soils the roots may penetrate below 2.7 m (9 ft). Trees without distinct taproots usually have lateral roots that turn and grow downward as they approach other trees. The bulk of the root system, however, consists of laterals confined largely to the upper 46 cm (18 in) of soil; much of the root system is in the upper 15 cm (6 in) of soil. In 25-year-old jack pine stands in central Wisconsin, the dry weight of all roots in the upper 1.5 m (5 ft) of soil was 10 980 to 13 790 kg/ha (9,800 to 12,300 lb/acre) *(61)*. A 40-year-old stand of jack pine in northern Minnesota produced 28 000 kg/ha (24,978 lb/acre), ovendry weight, of roots greater than 0.5 cm (0.2 in) and stumps less than 15 cm (6 in) tall *(73)*.

Reaction to Competition—Jack pine is one of the most shade-intolerant trees in its native range. It is the least tolerant of its associated pine species and is slightly more tolerant than aspen, birch, and tamarack. Jack pine may be more tolerant in the seedling stage and often requires some shade on dry sites to reduce surface temperatures and evapotranspiration. Soon after seedlings are established, however, they should receive full sunlight to assure survival *(10,61)*. Overall, jack pine can most accurately be classed as intolerant of shade.

Overstocked jack pine seedling and sapling stands with 4,950 or more trees per hectare (2,000/acre) should be weeded or cleaned (precommercial thinning) to improve growth and development. Otherwise such stands may stagnate because natural thinning in jack pine stands is slow except on the best sites *(10)*. A study in northern Minnesota, wherein direct seeding produced a stand averaging 32,100 trees per hectare (13,000/acre) at age 5 years, compared the growth of no thinning with thinning to square spacings of 1.2, 1.8, and 2.4 m (4, 6, and 8 ft). Twenty-two years later the treatments averaged 9, 10, 13, and 15 cm (3.7, 4.1, 5.1, and 5.8 in) in d.b.h., respectively *(14)*. Planting, direct seedings, and precommercial thinnings should have a goal of 2,000 to 3,000 trees per hectare (800 to 1,200/acre) by age 10 years *(19,30)*.

Jack pine is a pioneer species on burns or other exposed sites. In the absence of fire or other catastrophes, jack pine is succeeded by more tolerant species, but on the poorest, driest sites it may persist and form an edaphic climax. In loamy sands and sandy loams in northern Minnesota, the usual succession is from jack pine to red pine to eastern white pine to a hardwood type composed of sugar maple *(Acer saccharum)*, basswood *(Tilia americana)*, and northern red oak. Frequently, the red pine and white pine stages are absent and jack pine is followed by speckled alder *(Alnus rugosa)*, American hazel *(Corylus americana)*, beaked hazel *(C. cornuta)*, paper birch, and quaking aspen. This stage is followed by either the sugar maple-basswood association or spruce-fir. On loamy soils in northeastern Minnesota and parts of Canada, jack pine is succeeded by black spruce, white spruce, balsam fir, and paper birch. Eventually, the paper birch is eliminated from this association. In parts of northwestern Canada, jack pine may be replaced directly by white spruce; in parts of eastern Canada, the immediate succession may be to pure black spruce *(10,26,61)*.

Damaging Agents—Jack pine is subject to many agents that cause damage or mortality. Young jack pines are especially susceptible to early spring fires. Severe drought may kill many seedlings, particularly on coarse soils. All young jack pines less than 1.5 m (5 ft) tall and 55 percent of those from 1.5 to 3.7 m (5 to 12 ft) tall were killed by 123 days of flooding in northern Minnesota. Heavy populations of white-tailed deer can kill young jack pines up to 2.1 m (7 ft) tall, retard total height growth to half its potential, and deform most trees so they have little future value for timber products. Snowshoe hares can severely damage jack pine reproduction, particularly in dense stands in trees less than 4 cm (1.5 in) in d.b.h. *(16,61)*. Jack pine seedlings are greatly damaged by elk in western Manitoba when animal populations are high, and meadow voles cause occasional damage and mortality by gnawing the bark off main stems and lower branches *(16)*. Porcupines can cause extensive damage in older stands *(74)*.

Numerous insects affect the survival and growth of jack pine seedlings *(83)*. The more important groups of these are as follows: (1) root borers such as the pales weevil *(Hylobius pales)*, pine root collar weevil *(H. radicis)*, pine root tip weevil *(H. rhizophagus)*, and Warren's collar weevil *(H. warreni)*; (2) shoot and stem borers such as the northern pine weevil *(Pissodes approximatus)*, the white pine weevil *(P. strobi)*, and the Allegheny mound ant *(Formica exsectoides)*; (3) leaf feeders such as numerous sawflies *(Neodiprion sertifer, N. pratti banksianae, N. swainei, N. nigroscutum, N. compar, N. lecontei, N. dubiosus, N. nanulus nanulus), Diprion similis*, jack pine budworm, pine chafer *(Anomala oblivia)*, and pine webworm *(Tetralopha robustella)*; (4) needle miners such as *Argyrotaenia tabulana, Exoteleia* *pinifoliella*, and *Zelleria haimbachi;* (5) root feeders including primarily white grubs *(Phyllaophaga* spp.); and (6) sucking insects such as two midges *(Cecidomyia reeksi*, and *C. piniinopis)*, scale insects *(Nuculaspis california, Chionaspis pinifoliae*, and *Toumeyella parvicornis)*, spittlebugs *(Aphrophora parallela* and *A. saratogensis)*, and a wooly aphid *(Pineus coloradensis)*.

The jack pine tip beetle *(Conophthorus banksianae)* causes extensive shoot tip mortality, preferring sapling-size trees. The lodgepole terminal weevil *(Pissodes terminalis)* attacks and destroys the new terminal bud of jack pine in Saskatchewan *(61,83)*.

Several sawflies attack jack pine. Trees are often killed because the sawflies feed on both old and new needles. The pine tussock moth *(Parorgyia plagiata)* commonly defoliates large areas of sapling- and pole-size jack pine. The jack pine budworm is the most important defoliator of jack pine in the northeastern United States *(61,84)*.

Several diseases commonly attack young jack pines and reduce survival and growth. A needle rust fungus *(Coleosporium asterum)* causes some defoliation of seedlings. Diplodia blight *(Diplodia pinea)* frequently results in a shoot blight of jack pine seedlings under nursery conditions. Sirococcus shoot blight *(Sirococcus strobilinus)* has also caused seedling losses in Lake States nurseries. Scleroderris canker *(Gremmeniella abietina)* causes serious losses in both nursery stock and young plantations. Before nursery control programs for this disease were instituted in the Lake States, this fungus killed an average of 40 percent of seedlings in plantations established with infected stock *(77)*.

Jack pine is susceptible to a number of rust fungi that cause both growth loss and tree mortality. Many of these rusts are disseminated by infected nursery stock. The sweetfern blister rust *(Cronartium comptoniae)* sometimes kills many young seedlings and reduces the growth of survivors. More prevalent is the pine–oak (eastern) gall rust *(Cronartium quercuum)*, which may infect up to 50 percent of young seedlings, killing many of the seedlings with galls on the main stem. Young jack pine in Minnesota have been severely cankered by stalactiform rust *(Cronartium coleosporioides)*. In recent years the pine-to-pine (western) gall rust *(Endocronartium harknessii)* has been found throughout the Lake States in young jack pine stands. The importance of this rust is its potentially rapid rate of spread. This rust can infect directly from pine to pine without spending parts of its life cycle on an alternate host as do all the previously mentioned rusts *(77)*.

Sapling- and pole-size jack pine frequently show severe needlecast *(Davisomycella ampla)*. This fungus often causes loss of all but the current year's needles. Although affected trees suffer growth loss, the disease seldom causes mortality. Diplodia blight frequently kills branches and often the entire tree. This disease appears to be stress related and may reach epidemic status following drought. The European strain of scleroderris canker is currently killing many jack pine in northern New York and will cause serious losses if it reaches the major range of jack pine *(77)*.

The rust fungi mentioned under seedling disease also cause extensive mortality in pole-size stands. The pine–oak (eastern) gall rust has caused severe losses in jack pine stands in northern Wisconsin. In some pole-size stands the disease is so prevalent that the stands have become worthless and have been destroyed *(77)*.

The major root-rot fungi include the shoestring fungus *(Armillaria mellea)* and annosum root rot *(Heterobasidion annosum)* *(77)*.

The principal wood decay organisms are *Phellinus pini, Phaeolus schweinitzii*, and *Fomitopsis pinicola* *(77)*.

Windthrow is not a serious problem in jack pine stands except on shallow soils or when more than one-third of the stand basal area is removed in thinnings. Stem breakage from wind, ice, and snow is more common *(10)*.

Cone and seed production can be decreased by numerous factors. Red squirrels and other rodents destroy cones and consume seeds *(18,61,69,72)*. Low-vigor trees may produce much pollen but little seed. Pine–oak (eastern) gall rust damages trees resulting in smaller and aborted ovulate cones. Birds may be important consumers of jack pine seeds that fall to the ground or are directly sown *(61)*. Cone and seed insects may cause serious losses. In one study in northeastern Wisconsin, numerous insect species were found attacking conelets and cones *(57)*. The jack pine budworm *(Choristoneura pinus pinus)* destroyed 12 percent of the conelets. A mirid *(Platylygus luridus)* was observed piercing conelets as well as shoots and needles and was apparently responsible for a severe but unknown conelet abortion rate. The most prevalent insect attacking cones was the cone borer *(Eucosma monitorana)* which killed 10 percent of the cones. Other insects responsible for a total of about 4 percent cone mortality were the webbing coneworm *(Dioryctria disclusa)*, red pine cone beetle *(Conophthorus resinosae)*, jack pine budworm, and cone midges *(Lestodiplosis graddator, Resseliella silvana*, and *Asynapta hopkinsi)* *(57)*.

Other insects that directly damage jack pine conelets, cones, or seeds, or that decrease their numbers by damaging potential cone-bearing shoots include the jack pine tip beetle *(Conophthorus banksianae)*, shield-backed pine seed bug *(Tetyra bipunctata)*, Virginia pine sawfly *(Neodiprion pratti pratti)*, a moth *(Holcocera immaculella)*, eastern pine seedworm *(Laspeyresia toreuta)*, Nantucket pine tip moth *(Rhyacionia frustrana)*, European pine shoot moth *(R. buoliana)*, fir coneworm *(Dioryctria abietivorella)*, and spruce coneworm *(D. reniculelloides) (36)*.

Special Uses

The most notable special use for jack pine is as a breeding area for the Kirtland's warbler, a rare and endangered species. The Kirtland's warbler requires homogeneous stands of jack pine between 1.5 and 6 m (5 to 20 ft) tall (about 7 to 20 years old); stands are preferably larger than 32 ha (80 acres) *(52)*.

Jack pine stands can be an important part of the visual resource for recreation areas; they stabilize watersheds, produce areas for blueberry picking, and provide food and shelter for wild game species, including the snowshoe hare and the white-tailed deer *(10)*.

Genetics

The various environments in which jack pine grows over its wide range have provided ample opportunity for differentiation and natural selection *(72)*.

Virtually the entire present range of jack pine was glaciated during the most recent Wisconsin stage that reached its maximum about 18,000 years ago. The present distribution of the species therefore results from reinvasion and migration over huge areas and great distances in a relatively short time, estimated at 15,000 years since the retreat of the ice began in earnest. Available paleobotanical evidence suggests that jack pine survived the Wisconsin glacial maximum at low elevations in the Appalachian Mountains south of latitude 34° N. and also in the western Ozark Mountains. From these refugia it migrated to the north and east and up the Mississippi Valley, and westward around the southern end of the Lake Agassiz basin *(72)*.

Population Differences

The wide genetic variation found in the species suggests it has large effective breeding populations, heterozygosity for many alleles, and strong natural selection against self-fertilization and increased homozygosity *(72)*.

A study of 33 characteristics of tree crown, bark, wood, foliage, and cones of mature trees over most of the natural range showed that all varied significantly according to the geographic origin of the populations. An average of 37 percent of the variation was due to origin *(74)*. Environmental factors appear to be the dominant selection forces responsible for the natural variation over the present-day jack pine range. The area of optimum development of jack pine is north of the Great Lakes in Ontario and Quebec *(19,47)*.

Certain traits of jack pine have been demonstrated to be under strong genetic control including cone shape, cone serotiny, cone volume, cone length, scale number, number of scales to first ovule, and number of scales to first seed *(53,61,76,79)*. Early flowering appears to be under additive genetic control and not under the control of a single major gene or recessive genes *(41)*. Lammas growth and prolepsis, which may be detrimental to tree form, are under some genetic control *(62,63)*, and many of the traits contributing to desirable Christmas tree form are highly heritable *(55)*.

Races

Numerous jack pine provenance or seed source tests, established beginning in the early 1940's, have provided information on variation among provenances *(72)*. Studies of variation have included controlled environment chamber, greenhouse, nursery, and field experiment.

Growth, the characteristic most frequently emphasized in provenance studies, has been found to follow a generally clinal pattern associated with environmental gradients of latitude (photoperiod) and length and temperature of the growing season at the seed origin *(72)*. Differences in growth among provenances have been demonstrated beginning at the young seedling stage and by age 15 to 20 years the differences among provenances in tree growth and wood production are substantial *(72)*. For example, in a test of Lake States provenances at 14 locations, trees of two provenances from northeastern Minnesota were only 71 percent of the plantation mean height in a central Wisconsin plantation whereas trees of the tallest source, from Lower Michigan, exceeded the plantation mean by 17 percent after 20 years *(40)*. Translated to volume growth and considering tree survival, the volume per hectare of trees in the poorest provenances was only 38 percent of the plantation mean and that of the best was 187 percent of the plantation mean. These results clearly show the importance of selecting and using the best provenance or seed source in jack pine reforestation efforts and the magnitude of the losses in wood production that may result when seed origin is ignored. Provenance test results in Canada have similarly shown wide differences in growth among provenances *(72,84,85,86,87)*.

Most provenance tests show that trees of provenances from areas nearest the planting sites grow as well as or better than the average of trees of all provenances *(72)*. In the Lake States, however, trees of provenances that were moved slightly northward outgrew those of the local provenance *(40)*. Thus, although wide latitudinal movement of provenances is not suggested, movement up to 160 km (100 mi) northward in the Lake States can increase growth. Selection of superior provenances within latitudinal belts of similar climate should make substantial genetic gains possible *(72)*.

Biomass production of trees in 24- and 25-year-old plantations of four Lake States provenances at three locations ranged from 2.7 to 6.1 t/ha (about 1.2 to 2.7 tons/acre) annually *(89)*. Total biomass and mean annual biomass were negatively related to latitude of the plantation. Movement of provenances slightly northward within climatic zones resulted in increased biomass production of the trees but movement from warmer to colder short-growing-season zones resulted in poor growth.

Although tree growth has been the single most important trait evaluated in provenance tests, variation among provenances in other tree characteristics also has been noted. These include tree form as influenced by branching characteristics, wood and bark properties, cold hardiness, autumn foliage color variation in young seedlings, seed yield and quality, isozyme systems, and numerous instances of genetic variation in susceptibility or resistance to diseases and insect pests *(72)*.

The vast information available from provenance test results is being applied to the establishment of seed collection zones, breeding zones, and regional jack pine improvement programs in the Lake States *(44)* and in Canada *(72)*.

Hybrids

Although putative hybrids have been reported between jack pine and Virginia pine *(Pinus virginiana)*, loblolly pine *(P. taeda)*, and Japanese black pine *(P. thunbergiana) (72)*, jack pine × lodgepole pine *(P.* × *murraybanksiana* Righter and Stockwell) is the only verified interspecific hybrid in which jack pine is a parent *(59)*.

Widely scattered tests of the artificially created hybrids have shown mixed results, probably because the origin of the parents was not always matched with the environment of the test site *(25,50,58)*. Tests of the California-developed F_1 hybrids, F_2, backcross progeny, and the two parent species in northern Wisconsin and eastern Ontario showed that winter injury was associated with affinity to one or the other parent—it ranged from very severe in the lodgepole pine from California to none in the jack pine *(70,87)*. Polygenic inheritance was indicated suggesting that the backcross breeding method might be used to develop lines suitable for environments tolerated by the hardier parent.

The hybrids and the lodgepole parent were more susceptible to sweetfern rust and to eastern gall rust than local jack pine in tests in the Lake States and Ontario *(2,84)*. The form noted in some hybrids suggested some potential as Christmas trees but not as forest trees *(4)*. However, because of the high susceptibility to sweetfern rust reported in eastern and central Canada, the hybrids should not be planted in that region *(84)*.

Natural hybrids between jack pine and lodgepole pine occur in areas of contact in central and northwestern Alberta *(21,61,75)* and in scattered locations in Saskatchewan *(5,6)*. Differences in cone morphology provide the strongest diagnostic features for distinguishing the hybrids in the field *(61,72)*.

The turpentine of jack pine consists almost entirely of alpha- and beta-pinene but that of lodgepole pine is mostly beta-phellandrene with small amounts of 3-carene and the two pinenes. The hybrid contains one-fourth beta-phellandrene and three-fourths pinenes. Thus, in the F_1 hybrids the bicyclic terpenes of jack pine dominate over the simpler monocyclic terpene of lodgepole pine in a 3-to-1 ratio *(61)*. Further study of the segregation for turpentine components in the hybrids suggested that the composition is probably controlled primarily by a limited number of genes with major effects *(88)*. Discrimination between lodgepole pine and putative hybrids with jack pine based on analysis of monoterpenes showed that the transition zone between the species may be farther west than previously reported *(56)*.

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Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg. **Sand Pine**

Pinaceae Pine family

R. H. Brendemuehl

Sand pine *(Pinus clausa)* is also known as scrub pine and spruce pine. The majority of trees in natural sand pine stands of western Florida, especially between Panama City and Pensacola, bear cones that open when mature. These stands tend to be uneven-aged, somewhat open, with abundant reproduction developing in the openings. Sand pine stands in eastern and central Florida are generally dense and even-aged with a majority of the trees bearing serotinous cones. Two geographic races have been distinguished on the basis of cone characteristics: Ocala (var. *clausa*) from northeastern to south Florida and Choctawhatchee (var. *immuginata* D. B. Ward) in northwest Florida and Baldwin County, AL *(25)*.

Habitat

Native Range

Sand pine (fig. 1) is one of the minor southern pines with a natural range limited almost entirely to Florida. The largest sand pine concentration is a block of the Ocala variety covering about 101 170 ha (250,000 acres) in north-central Florida, an area often referred to as the "Big Scrub." This variety of sand pine also grows in a narrow strip along the east coast of Florida from St. Augustine southward to Fort Lauderdale. On the Gulf Coast small tracts of Ocala sand pine can be found scattered from a few kilometers north of Tampa southward to Naples. The less abundant Choctawhatchee variety is found growing along the coast in western Florida from Apalachicola to Pensacola and extending westward into Baldwin County, AL. Natural stands of Choctawhatchee sand pine are most abundant in Okaloosa and Walton Counties, FL, covering an area of about 40 470 ha (100,000 acres). Scattered stands of this variety of sand pine can be found 32 to 40 km (20 to 25 mi) inland from the coast in this section of Florida. Sparse stands of sand pine are also found on many of Florida's offshore islands *(15,24)*.

Climate

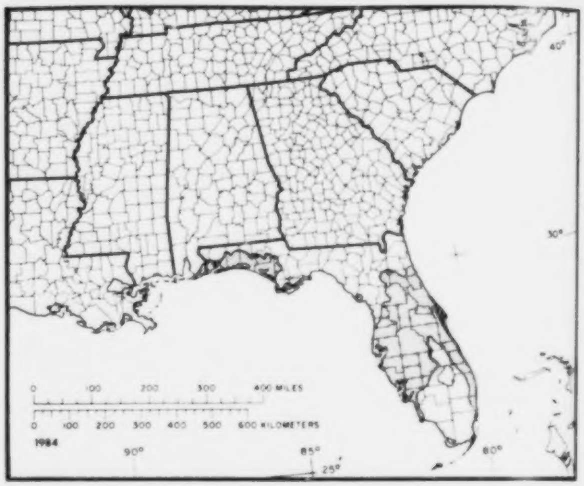

Figure 1—*The native range of sand pine.*

The climate of north-central Florida is characterized by hot summers with abundant precipitation and mild, rather dry winters. Precipitation varies from 50 to 75 mm (2 to 3 in) per month from October until April to as much as 200 to 230 mm (8 to 9 in) per month in June, July, and August. About 55 percent of the average rainfall of 1350 mm (53 in) occurs in the 4 months from June through September. Temperature extremes of -11° and 41° C (12° and 105° F) have been recorded. A frost-free period of 290 days is normal.

Choctawhatchee sand pine thrives in western Florida under climatic conditions that are somewhat different from those of north-central Florida. Rainfall from December through May averages 100 to 110 mm (4 to 4.5 in) per month. It is hot and humid from June through September but slightly less so than in the north-central area. About 43 percent of the average annual rainfall of 1520 mm (60 in) occurs during this period of the year. October and November are the driest months, with rainfall averaging about 75 mm (3 in) per month. Temperature extremes of -17° and 42° C (2° and 107° F) have been recorded. Average temperature for January is 11° C (52° F) and 27° C (81° F) for July. A frost-free period of 265 days is normal *(23)*.

Soils and Topography

Sand pine grows on well-drained to excessively drained, infertile, acid to strongly acid sandy soils of

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the order Entisols. This sand is of marine origin, much of which was deposited in terraces developed during the Pleistocene epoch.

Most Ocala sand pine grows in the division of Florida known as the Central Highlands. Elevations range from less than 6 m (20 ft) above sea level near Lake George to nearly 61 m (200 ft) in the highest areas of this region. Numerous lakes dot this area and are indicative of the presence of soluble limestone not far below the surface. Gentle rolling hills characterize the terrain. The major soils on which Ocala sand pine grows, in order of importance, are the Astatula, Paola, and St. Lucie series *(1)*.

In west Florida, scattered stands of Choctawhatchee sand pine grow on the excessively drained soils of the Coastal Lowlands; however, the majority of such stands are in the division of Florida known as the Western Highlands (fig. 2) *(10)*. Elevations range from near sea level to nearly 90 m (295 ft) above sea level. The terrain of this area is typified by long, gentle slopes and broad, nearly level ridgetops. Sloping to steep hillsides border most of the streams and small lakes of the area. The water level of the rivers, lakes, and intermittent ponds of the area fluctuates considerably according to the amount of rainfall and seepage from the surrounding deep, sandy soils. Soils common to this region include the Kershaw and Lakeland series.

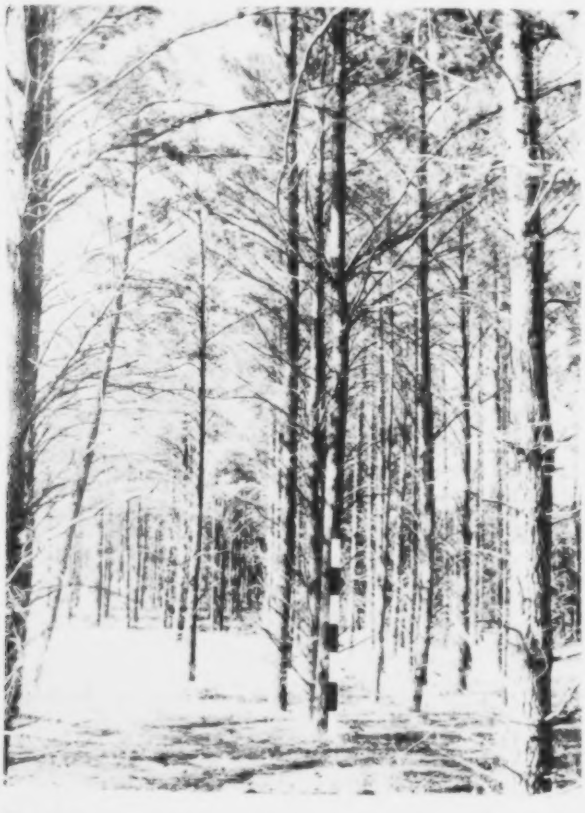

Figure 2—*Twenty-eight-year-old plantation of Choctawhatchee sand pine on Elgin Air Force Base in western Florida.*

Associated Forest Cover

The sand pine scrub of north-central Florida is one of the most distinctive plant communities of the State. Of particular interest is the sharpness of the boundaries with the adjacent sandhill vegetation which is dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and pineland threeawn (*Aristida stricta*). Even-aged Ocala sand pine dominates the overstory, while the understory is composed almost entirely of evergreen shrubs 1.8 to 3.0 m (6 to 10 ft) tall. There is little or no herbaceous ground cover. Shrubs found in this understory include sand live oak (*Quercus virginiana* var. *geminata*), myrtle oak (*Q. myrtifolia*), Chapman oak (*Q. chapmanii*), rosemary (*Ceratiola ericoides*), tree lyonia (*Lyonia ferruginea*), scrub palmetto (*Sabal etonia*), saw-palmetto (*Serenoa repens*), silk bay (*Persea borbonia* var. *humilis*), gopher-apple (*Chrysobalanus oblongifolius*), and ground blueberry (*Vaccinium myrsinites*). Mats of lichens (*Cladonia* spp.) are often plentiful on the ground beneath the trees and shrubs *(14)*.

The west Florida sand pine scrub is a distinct contrast to that of the north-central area. Here Choctawhatchee sand pine generally grows in uneven-aged stands and invades adjacent forested sites if protected from uncontrolled fire. The understory in these stands is quite sparse. Turkey oak, bluejack oak (*Q. incana*), sand post oak (*Q. stellata* var. *margaretta*), pineland threeawn, and prickly pear (*Opuntia* spp.) are the most common species of this understory.

Sand pine is the principal component of the forest cover type Sand Pine (Society of American Foresters Type 69) *(12)*. It may also be found in several additional cover types such as Longleaf Pine (Type 70), Longleaf Pine–Scrub Oak (Type 71), and Slash Pine (Type 84).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sand pine is monoecious. Flower buds are formed early in the summer but do not become visible until early autumn. The

Table 1—Cone and seed characteristics of sand pine (*Pinus clausa*)

Characteristic	Choctawhatchee (var. *immuginata*)	Ocala (var. *clausa*)
Cones	Most cones open	Most cones remain closed
Number per liter	28	24
Number per bushel	1,000	830
Seed per cone	42	37
Sound seed		
Number per kilogram	25,447	21,410
Number per pound	56,100	47,200
Clean seed		
Weight per 35 liters of cones	0.27 kg	0.27 kg
Weight per bushel of cones	0.6 lb	0.6 lb
Dormancy	Mildly dormant	Nondormant
Germination		
No pretreatment	88%	94%
Stratified[1]	93%	96%
Peak, unstratified	17 days	10 days
Peak, stratified	11 days	9 days

[1] For stratification, seeds were placed in germination dishes containing a 1 to 2 mixture of moist sand and peat moss and refrigerated at 1° C (34° F) for 14 days.

time when staminate flowers ripen, as shown by pollen release, is one of the more reliable phenological events distinguishing the two varieties of sand pine. Ocala sand pine grows throughout most of the peninsula of Florida between latitude 26° and 30° N. At the southern end of its range it may start shedding pollen as early as mid-November but could start a month or more later in northern Florida. In plantations of Ocala in northwest Florida, pollen generally is shed from the last weeks of December through mid-January. By contrast, the Choctawhatchee variety of sand pine grows naturally only in northwest Florida, essentially within 1 degree of latitude. Pollen dissemination by this variety may start as early as the last week of December and end as late as mid-March but occurs most frequently from late January through February. There is little overlap in the periods when the two varieties shed pollen *(6)*. Conelet development is minimal during the first year but increases rapidly during the second year. Cones attain mature size by late summer.

Seed Production and Dissemination—Sand pine bears cones at an early age. It is not unusual to find mature cones on 5-year-old trees. Occasionally flowers, usually pistillate strobili, are produced by 9- to 10-month-old seedlings growing under nursery conditions. The two varieties of sand pine differ appreciably in cone production, cone size, seed size, and several other characteristics. An abundant crop of cones is produced by Ocala sand pine almost annually. Choctawhatchee cone crops of similar size are produced at 4- to 6-year intervals, with light crops in intervening years. Other differences of note are listed in table 1 *(2)*.

The majority of Ocala sand pine cones are serotinous: they remain closed when mature and require heat to open. Consequently, seed dispersal is minimal. The cones are very persistent and may accumulate in large numbers on a single tree. Viability of the seeds in such cones decreases with age; only 10 to 20 percent of the seeds in 5-year-old cones may be viable. Seeds from cones 2 or more years old have also been shown to be relatively dormant as compared to newer seeds *(24)*.

Overly dense, unmanaged stands of the Ocala sand pines have developed following wildfire, which causes the cones to open and release large quantities of seeds *(11)*. Regeneration methods based on cone serotiny have had limited success. Stands to be regenerated are clearcut, the slash and residual vegetation are chopped, and mineral soil is exposed with site preparation equipment such as rolling drum choppers. Cones in close proximity to the soil open and release their seeds when exposed to high surface soil temperatures. Uniform distribution of seeds from treetops is difficult to attain, and poorly regenerated stands often result. Direct seeding at a rate of 0.56 to 1.12 kg/ha (0.5 to 1.0 lb/acre) after site preparation has been the most practical and successful regeneration method. This operation is most successful if the seeds are distributed from October through January and covered with about 6 mm (0.25 in) of soil shortly after being distributed *(16)*.

Seed dissemination of Choctawhatchee sand pine differs from that of Ocala sand pine. The majority of Choctawhatchee cones open when mature and most of the seeds are disseminated during September, October, and November. In western Florida the prevailing winds during the fall are from the west and northwest, and consequently seeds are distributed more evenly and to a greater distance on the eastern and southeastern sides of stands of seed-bearing age. It has been reported that along the western edge of a plantation, sand pine seedlings became established in the scrub oak–wiregrass cover for a distance of only 23 m (75 ft), or approximately 1.5 times average tree height (16.5 m or 54 ft at age 28). East of this plantation, reproduction was established in sufficient numbers to form a well-stocked stand for a distance of 38 m (125 ft). Occasional Choctawhatchee sand pine seedlings were noted beyond the bounds of the sample area (105 m or 345 ft) in all but a northwesterly direction from the seed source *(7)*.

Regeneration of this variety of sand pine may be accomplished quite simply. Cuttings can be timed to take advantage of its seed-dissemination characteristics, and as the seedlings can become established in competition with both understory and overstory vegetation, a natural system such as the shelterwood is a comparatively reliable and inexpensive regeneration method *(5)*.

Seedling Development—Seedlings of the two varieties of sand pine differ markedly in their development, but germination of both is epigeal. Peak germination of Ocala seed occurs within 10 days after the seed is sown in the nursery, while Choctawhatchee seed requires 17 to 21 days. The Ocala seedlings grow more rapidly than Choctawhatchee and are often 38 to 46 cm (15 to 18 in) tall at the end of the growing season. Choctawhatchee seedlings usually attain an average height of about 25 to 38 cm (10 to 15 in) in the same period of time. This difference in rate of height growth may continue for 2 to 3 years after the seedlings have been transplanted to the field; however, average annual height growth of both varieties is essentially identical by the time the trees are 4 to 5 years old.

Maximum germination of seed distributed naturally or by direct seeding occurs from November through January for both varieties. Root development is rapid, and, as a result, seedling mortality is especially low when seedlings become established on bare areas during this period of the year. Germination from natural seed dispersal or direct seeding may occur at any time of the year, but few seeds disseminated during the summer months produce seedlings. High soil temperature may be a limiting factor. Surface soil temperatures as high as 72° C (162° F) have been observed in June and July on sandhill sites in Florida *(8,24)*.

Two flushes of growth are common during the first year of seedling development. The first occurs early in spring and the second usually in September and October. This growth characteristic is of special significance to the nurseryman. Sand pine seedlings, especially the Choctawhatchee variety, typically are only 10 to 13 cm (4 to 5 in) tall as late in the growing season as mid-August. Nothing need be done to stimulate such seedlings to attain plantable size as 1-0 seedlings. The application of nitrogen at this time produces exceptionally large, often succulent seedlings that are difficult to plant and not well suited to the rigors of the sandhill environment *(4)*. Once established in the field, 3- to 4-year-old sand pines typically have three and occasionally four growth flushes during a single growing season. The fourth elongation generally occurs early in fall and is triggered by favorable soil moisture conditions.

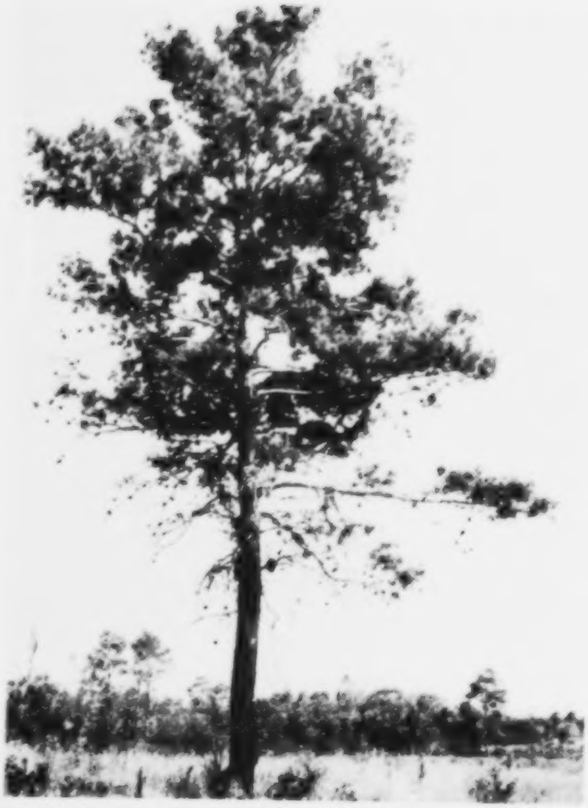

Figure 3—*Open-grown Ocala sand pine.*

Birds, mammals, and insects cause the greatest losses of sand pine seeds and damage to newly germinated seedlings. The primary predators change with the season; losses attributed to migratory birds are greatest during spring and fall, while losses to insects and small mammals increase during the spring and summer as their numbers increase. Ants are more numerous and probably more destructive than all other insects. Birds and ants may be responsible for most seedling losses to predators *(8)*.

Vegetative Reproduction—Sand pine does not reproduce vegetatively. Seedlings of the Choctawhatchee variety do produce poorly developed basal branches. When 1- to 2-year-old seedlings are injured or decapitated, one or more of these basal branches may elongate and replace the lost terminal.

Sand pine has been successfully grafted by several methods. Scion material from both sand pine varieties obtained from 20- to 60-year-old trees has been grafted successfully to potted slash, Ocala sand, and Choctawhatchee sand pine root stock as well as to root stocks of these same species growing in nursery beds. A wedge or cleft graft is commonly used *(3)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Sand pine (fig. 3) varies in size from the unmerchantable scrub growing on the coastal sand dunes of Florida to trees that attain saw-log size on the better sites. Trees ranging from 51 to 66 cm (20 to 26 in) in d.b.h. and 23 to 26 m (75 to 85 ft) in height are found on the best sites but smaller sizes are more common. The largest sand pine in Florida, for example, is 63 cm (24.8 in) in d.b.h. and 31.4 (103 ft) tall.

Most of the volume of sand pine is currently being harvested for pulpwood, but the construction lumber market is a good potential outlet for some of the volume of sand pine. Formerly, tree size may have been a deterrent to its use for structural lumber, but improved sawmill equipment can now handle large volumes of small logs 15 to 25 cm (6 to 10 in) in diameter inside bark to produce lumber suitable for construction purposes. Both varieties have sufficient density for this use. Actually the density of Choctawhatchee is somewhat higher than that of Ocala. It could be put to structural uses similar to those of loblolly *(Pinus taeda)* and shortleaf *(P. echinata)* pines because the specific gravity of all three is in the same range *(22)*.

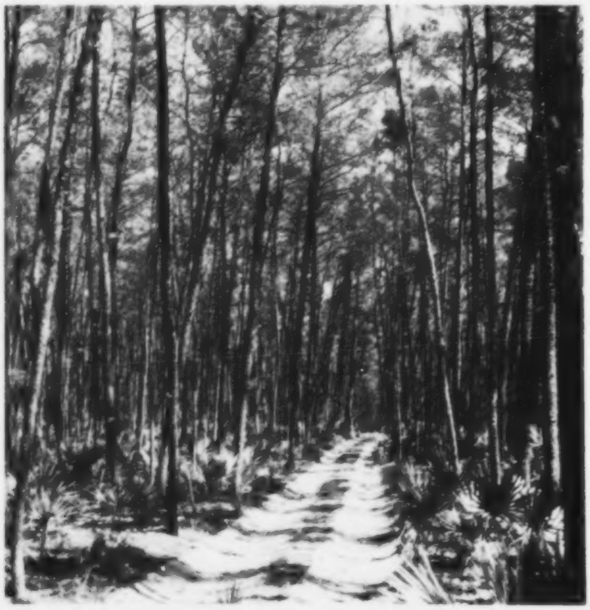

Figure 4—*Dense natural stand of 35- to 40-year-old Ocala sand pine on Ocala National Forest, FL.*

On the best sites, site index 24.4 m or 80 ft (age 50 years), the dominant trees in Ocala sand pine stands are expected to average 38 to 46 cm (15 to 18 in) in d.b.h. and 24 m (80 ft) in height. On average sites, site index 18.3 m or 60 ft, the dominant trees should average 25 to 30 cm (10 to 12 in) in d.b.h. and 18 m (60 ft) in height (fig. 4). The dominant stand on the poor sites, site index 15.2 m or 50 ft, is expected to average 18 to 23 cm (7 to 9 in) in d.b.h. and 15 m (50 ft) in height when mature.

In well-stocked natural stands of Ocala sand pine, yields of 126, 94, and 63 m^3/ha (20, 15, and 10 cords/acre) are predicted for high, average, and poor sites, respectively, at a rotation age of 40 to 45 years *(21)*. These stands tend to break up markedly when they are 50 to 60 years old. Yield tables or site index curves have not been prepared for Choctawhatchee sand pine but a limited amount of information is available. Well-stocked natural stands are expected to produce 210 m^3/ha (15,000 fbm/acre) of merchantable sawtimber plus 63 m^3/ha (10 cords/acre) of pulpwood *(5)*. Yields of Choctawhatchee plantations are expected to exceed the volumes reported above for Ocala sand pine. On the basis of data obtained from a very limited number of 25-year-old plantations, merchantable volumes for high, average, and poor sites, to a 7.6-cm (3-in) diameter outside bark, are anticipated to be 252, 189, and 126 m^3/ha (40, 30, and 20 cords/acre) for 25- to 30-year rotations.

Rooting Habit—Sand pine seedlings grown on very sandy sites develop a very fine root system with numerous laterals. The root system is somewhat coarser when the seedlings are grown on heavier textured soils; however, sand pine root systems are generally much finer and have greater development of lateral roots than is typical of other southern pines. Information is lacking on the rooting habit of sand pine older than seedlings.

Reaction to Competition—Sand pine has been rated as being moderately intolerant of shade and competition, but in its early establishment it is quite tolerant. Overall, it probably is most accurately classed as having intermediate tolerance to shade. Sand pine expresses very little dominance in its usual growth pattern. Sand pine grows and persists in very dense stands of approximately 20,000 to 25,000 trees per hectare (8,000 to 10,000/acre). Seedlings of both varieties can be planted or will become established from seed in the scrub oak–wiregrass rough common to the Florida sandhills and eventually dominate the site. Natural pruning is very slow. Dead lateral branches may persist within a few feet of the ground until the trees are 20 to 25 years old.

Damaging Agents—Insects, disease, and fire play a significant role in the development of sand pine stands. Several species of insects attack and kill, deform, or cause growth losses of sand pine. Most of these pests, the majority of which also attack the other species of pine growing in Florida, are found throughout the range of sand pine.

Bark beetles, primarily Ips (*Ips calligraphus* and *I. grandicollis*), probably cause the greatest volume loss in sand pine, especially the Choctawhatchee variety. Generally, stress factors such as severe drought, lightning, fire, mechanical damage, or crowded stand conditions are associated with Ips beetle attacks.

The sand pine sawfly (*Neodiprion pratti*) is considered a potential cause of growth loss in sand pine. Plantations of both varieties of sand pine have been defoliated by this insect. Attacks are reported to be most severe along stand edges and in plantations with fewer than 750 trees per hectare (300/acre) *(27)*. Outbreaks of the blackheaded pine sawfly (*N. excitans*) on sand pine, concurrent with localized outbreaks of this sawfly on loblolly pine in northwest peninsular Florida, have also been reported *(26)*. The pitch-eating weevil (*Pachylobius picivorus*) and the pales weevil (*Hylobius pales*) could become important insect pests of sand pine, but future losses will depend on management practices.

Tip moths (*Rhyacionia* spp.), aphids, and scales have all been observed on sand pine but are not known to cause mortality or appreciable growth loss. These insects do cause a certain amount of deformity and discoloration of young trees and could cause significant losses where the objective of management is Christmas tree production. The southern pine coneworm (*Dioryctria amatella*) frequently damages twigs and cones, and if uncontrolled may cause substantial losses in seed orchards and seed production areas *(9)*.

Sand pine varies in its susceptibility to disease. Mushroom root rot caused by *Clitocybe tabescens* is found in natural stands of Ocala sand pine in central Florida and also has developed in Ocala plantations in northwest Florida and southern Georgia during the past 5 to 10 years *(18)*. As a result of this disease, a significant portion of many Ocala plantations may not reach merchantable size. The Choctawhatchee variety is considered resistant to this disease. *Phytophthora cinnamomi* is reported to be a virulent pathogen on seedlings of both the Ocala and Choctawhatchee varieties of sand pine, but there is no conclusive proof that this fungus is a pathogen of sand pine under field conditions. Heavy clay or poorly drained soils may support populations of *P. cinnamomi*. The areas of Florida and Georgia where planted sand pines have been killed by *Clitocybe tabescens* and where *Phytophthora cinnamomi* was later recovered were either shallow soils underlain by clay or were imperfectly drained sandy soils. Such soil conditions are not characteristic of a sand pine site. Eastern gall rust (*Cronartium quercuum*), which forms spherical galls mainly on twigs and branches of both sand pine varieties, is common but seldom a serious problem. Heart rot caused by *Phellinus pini* has been reported in sand pine but is usually not a problem until the stands are more than 40 years old *(19)*.

Fire is probably the principal enemy of sand pine, which is much less fire resistant than longleaf or slash pine. Hot ground fires which produce substantial needle scorch kill as readily as crown fires, yet sand pine can be burned under controlled conditions. This is especially true of Choctawhatchee variety, as its natural understory vegetation tends to be less flammable than that generally found in natural stands of the Ocala variety.

A unique combination of fuel and weather conditions appears to be responsible for the occasional blowup fires that occur in Ocala sand pine forests. The moisture content of sand pine needles is often lowest in March, and their resin and energy contents reach a yearly high from February through May. This condition is known as the "varnish stage" by those familiar with fire in Ocala stands. These fuel properties take on critical importance when they are combined with severe drought conditions and blustery spring weather characterized by unstable air masses, low relative humidity, and high winds.

The relation between Ocala sand pine and fire is somewhat of a paradox. Many acres of Ocala sand pine forest owe their existence to fire which releases seed from the serotinous cones. As a considerable volume of timber may be lost to such fires, however, this method of regeneration cannot be considered an acceptable form of management *(11)*.

Special Uses

Using sand pine for fuelwood or biomass plantations is feasible. Production levels comparable to those attained by other biomass species can be produced in plantations established at spacings of 0.6 by 1 m (2 by 3 ft). Annual dry weight yields of 7.13 t/ha (3.18 tons/acre) have been produced on 17-year-old Choctawhatchee sand pine plantations *(17)*.

Some sand pines, especially the Choctawhatchee variety with its short, heavily foliated branches and dark green needles, are being grown for Christmas trees. Marketable trees 2 to 3 m (7 to 10 ft) tall can be produced in 4 to 5 years.

Genetics

The two geographic races of sand pine have been identified earlier in this paper.

Natural hybridization of sand pine has not been known to occur, but several successful attempts at artificial hybridization have been reported. The most encouraging of these efforts is a cross between Virginia pine *(P. virginiana)* and the Choctawhatchee variety of sand pine produced at the Institute of Forest Genetics at Placerville, CA, in 1953. Seedlings from this cross were planted in Charles County, MD. At age 10, 94 percent (47 trees) of the hybrid seedlings had survived, with an average height of 5.4 m (17.6 ft). Survival of the Virginia pine controls averaged 84 percent with an average height of 4.8 m (15.6 ft). These results indicate the feasibility of moving sand pine germ plasma into more northerly locations through hybridization with Virginia pine *(20)*.

Attempts to move sand pine north of its natural range without benefits of hybridization are also encouraging. Identical studies in the Georgia and South Carolina sandhills show that sand pines grow better than loblolly, longleaf, and slash pine *(P. elliottii)* on these deep, droughty, infertile sands. Heights at age 15 years averaged 10.8 m (35.4 ft) for Choctawhatchee sand pine, 10.0 m (32.8 ft) for Ocala sand pine, and 7.32 m (24.0 ft), 7.25 m (23.8 ft), and 6.9 m (22.6 ft) for slash pine, longleaf pine, and loblolly pine. Ice storms have caused the most serious damage to the Ocala plantings, but damage to the Choctawhatchee plantings from these same storms has been no greater than that done to longleaf and slash pine. The growth rate of Choctawhatchee sand pine included in these tests is comparable to that for plantations of this variety growing in northwest Florida *(13)*.

Several organizations have attempted a number of additional crosses with sand pine and other species of pine *(20)*. Slash pine × Ocala sand pine crosses were generally unsuccessful. Reported crosses in which the sand pine parent was not identified by variety included these:

P. taeda × *P. clausa*
P. clausa × *P. taeda*

P. banksiana × *P. clausa*
P. clausa × *P. banksiana*

P. rigida × *P. clausa*
P. clausa × *P. rigida*

P. pungens × *P. clausa*

P. pinaster × *P. clausa*
P. clausa × *P. pinaster*

P. echinata × *P. clausa*
P. clausa × *P. echinata*

P. virginiana × *P. clausa*
P. clausa × *P. virginiana*

P. thunbergii × *P. clausa*

P. clausa × *P. clausa*

With the exception of *P. virginiana* × *P. clausa* and *P. clausa* × *P. virginiana*, these crosses produced few sound seeds per cone. The *P. virginiana* × *P. clausa* cross produced an average of 13.1 sound seeds per cone, a yield that compares favorably with the results of many artificial intraspecific crosses. If such results are generally obtainable, mass production of this hybrid may be possible (20).

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Pinus contorta Dougl. ex. Loud. Lodgepole Pine

Pinaceae Pine family

James E. Lotan and William B. Critchfield

Lodgepole pine (*Pinus contorta*) is a two-needled pine of the subgenus *Pinus*. The species has been divided geographically into four varieties: *P. contorta* var. *contorta*, the coastal form known as shore pine, coast pine, or beach pine; *P. contorta* var. *bolanderi*, a Mendocino County White Plains form in California called Bolander pine; *P. contorta* var. *murrayana* in the Sierra Nevada, called Sierra lodgepole pine or tamarack pine; and *P. contorta* var. *latifolia*, the inland form often referred to as Rocky Mountain lodgepole pine or black pine. Although the coastal form grows mainly between sea level and 610 m (2,000 ft), the inland form is found from 490 to 3660 m (1,600 to 12,000 ft).

Habitat

Native Range

Lodgepole pine (fig. 1) is an ubiquitous species with a wide ecological amplitude. It grows throughout the Rocky Mountain and Pacific coast regions, extending north to about latitude 64° N. in the Yukon Territory and south to about latitude 31° N. in Baja California, and west to east from the Pacific Ocean to the Black Hills of South Dakota. Forests dominated by lodgepole pine cover some 6 million ha (15 million acres) in the Western United States and some 20 million ha (50 million acres) in Canada.

Climate

Lodgepole pine grows under a wide variety of climatic conditions *(52)*. Temperature regimes vary greatly. Minimum temperatures range from 7° C (45° F) on the coast to -57° C (-70° F) in the Northern Rocky Mountains. Maximum temperatures range from 27° C (80° F) along the coast and at high elevations to well over 38° C (100° F) at low elevations in the interior. Average July minimums frequently are below freezing at high elevations. Lodgepole seedlings are relatively resistant to frost injury in some locations *(16,42)* and often survive in "frost-pockets" where other species do not.

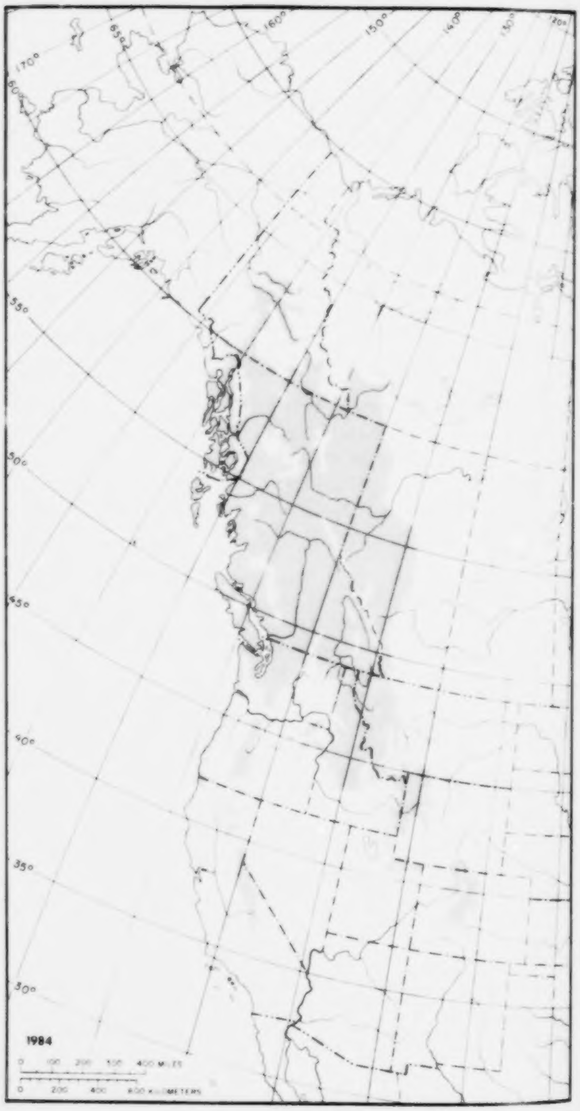

Figure 1—*The native range of lodgepole pine.*

At low elevations in the interior, lodgepole pine grows in areas receiving only 250 mm (10 in) of mean annual precipitation, whereas it receives more than 500 mm (200 in) along the northern coast. Many interior sites often are low in summer rainfall.

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Seasonal distribution of precipitation is significant; snowfall supplies most of the soil water used for rapid growth in early summer. Temperatures are frequently favorable for germination after snowmelt, and germination occurs rapidly. Lodgepole is very intolerant of shade and generally grows best in full sunlight.

Soils and Topography

Lodgepole pine grows on soils[1] that vary widely but are usually moist. Growth is best where soil parent materials are granites, shales, and coarse-grained lavas *(24,27)*; other soils have developed from glacial till of widely varying composition, Recent, Tertiary, and Oligocene alluvium and colluvium (from such sources as quartzites and argillites), limestone of the Belt geologic series, pumice, and volcanic ash. Lodgepole pine is seldom found on the generally drier soils derived from limestone. In Canada, however, extensive stands occur on calcareous glacial tills *(56)*. Glacial drift provides a balance of moisture and porosity on which the species seems to thrive, as in Alberta, where it grows better on glacial tills than on alluvial soils or lacustrine deposits. In Montana, highly calcareous soils derived from dolomitic limestone usually do not support lodgepole pine, subalpine fir *(Abies lasiocarpa)*, and Engelmann spruce *(Picea engelmannii)*, although they do support Rocky Mountain Douglas-fir *(Pseudotsuga menziesii* var. *glauca)*. Nevertheless, soils developed in colluvium from other types of limestone and calcareous glacial till do support stands of lodgepole pine.

Extensive stands of lodgepole pine (var. *latifolia*) occur on soils classified as Inceptisols or Alfisols in the interior forests. Although the species commonly grows on Andepts and does well on these soils in some areas, the Boralfs and Ochrepts probably support better tree development and more extensive stands. Frequently lodgepole pine soils on Boralfs and Ochrepts have cryic soil temperature regimes. In the Blue Mountains of Oregon lodgepole pine does well on Andepts, where it is nearly always found on volcanic ash or alluvial material overlying residual basaltic soils, at elevations between 910 and 2130 m (3,000 and 7,000 ft). The ash cap soils are deeper and hold more moisture than the residual soils.

The coastal form of lodgepole pine (var. *contorta*) is often found on Histosols (peat bogs or muskegs) in southeastern Alaska, British Columbia, and western Washington, and on dry, sandy, or gravelly sites farther south along the coast on Inceptisols, Alfisols, and Ultisols.

Soil properties and soil moisture often favor lodgepole pine locally over other species. Lodgepole pine grows on wet flats and poorly drained soils in the Cascade Range in Washington and Oregon, and the Sierra Nevada in California. Soils with underlying hardpan support lodgepole pine to the exclusion of such species as ponderosa pine *(Pinus ponderosa)*, redwood *(Sequoia sempervirens)*, or Douglas-fir in the Sierra Nevada, eastern Oregon, and Mendocino County, CA. Lodgepole pine also grows on level sites with and without high water tables in central Oregon where frost tolerance during germination allows its establishment to the exclusion of other species. Extensive stands are found in these areas on well drained sites above 1600 m (5,250 ft), with patterns of occurrence attributed to past fires.

On infertile soils, lodgepole pine is often the only tree species that will grow. Nevertheless, experiments have demonstrated significant growth increase from fertilization, particularly nitrogen *(15)*.

Lodgepole pine thrives in a wide variety of topographic situations. It grows well on gentle slopes and in basins, but good stands are also found on rough and rocky terrain and on steep slopes and ridges, including bare gravel. Northern and eastern slopes are more favorable than southern and western aspects *(3)*.

Associated Forest Cover

Lodgepole pine grows both in extensive, pure stands, and in association with many western conifers. The forest cover type Lodgepole Pine (Society of American Foresters Type 218) *(26)* exists as a pure (80 percent or more) component of basal area stocking, as a majority (50 percent or more), or as a plurality (20 percent or more). The cover type includes all recognized subspecies of *Pinus contorta*.

Lodgepole pine is a component in 27 of the 55 SAF western forest cover types. In the Northern Interior (Boreal) group it is represented in White Spruce (Type 201), White Spruce–Aspen (Type 251), White Spruce–Paper Birch (Type 202), Paper Birch (Type 252), and Black Spruce (Type 204).

It is a component in all six high elevation cover types: Mountain Hemlock (Type 205), Engelmann Spruce–Subalpine Fir (Type 206), Red Fir (Type 207), Whitebark Pine (Type 208), Bristlecone Pine (Type 209), and California Mixed Subalpine (Type 256). At middle elevations in the interior it is a minor component of seven other types: Interior Douglas-Fir

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[1] Soils were classified in consultation with Richard Cline of the USDA Forest Service, Forest Environment Research Staff, Washington, DC; Hal Hunter of the Soil Conservation Service, Bozeman, MT; and Carl Davis, Gallatin National Forest, Bozeman, MT..

(Type 210), Western Larch (Type 212), Grand Fir (Type 213), Western White Pine (Type 215), Blue Spruce (Type 216), Aspen (Type 217), and Limber Pine (Type 219). In the North Pacific forests, it is a component in Coastal True Fir (Type 226), Western Redcedar–Western Hemlock (Type 227), Western Redcedar (Type 228), Douglas-Fir–Western Hemlock (Type 230), Port Orford-Cedar (Type 231), and Redwood (Type 232). At low elevations in the interior it is associated with Interior Ponderosa Pine (Type 237) and in the South Pacific forests it is a component of Jeffrey Pine (Type 247).

Lodgepole pine, with probably the widest range of environmental tolerance of any conifer in North America, grows in association with many plant species *(30,50,59,60)*. The lodgepole pine forest type is the third most extensive commercial forest type in the Rocky Mountains.

Lodgepole pine's successional role depends upon environmental conditions and extent of competition from associated species. Lodgepole pine is a minor seral species in warm, moist habitats and a dominant seral species in cool dry habitats. It is often persistent even on cool and dry sites and can attain edaphic climax at relatively high elevations on poor sites. Fire regimes have played a role in this successional continuum, especially where repeated fires have eliminated a seed source for other species *(27)*. Lodgepole pine may even overwhelm a site with seed stored in serotinous cones. It has four basic successional roles *(50)*:

Minor Seral–A component of even-aged stands rapidly being replaced by shade-tolerant associates in 50 to 200 years.

Dominant Seral–The dominant cover type of even-aged stands with a vigorous understory of shade-tolerant species that will replace lodgepole pine in 100 to 200 years.

Persistent–The dominant cover type of even-aged stands with little evidence of replacement by shade-tolerant species.

Climax–The only tree species capable of growing in a particular environment; lodgepole pine is self-perpetuating.

Life History

The following statements apply principally to lodgepole pine in the most important part of its range; namely northern Colorado, Wyoming, Montana, northern Utah, Idaho, eastern Oregon, western Alberta, and southern British Columbia.

Reproduction and Early Growth

Flowering and Fruiting—Male and female strobili generally are borne separately on the same tree in this monoecious species, with female flowers most often at the apical end of main branches in the upper crown, and male flowers on older lateral branches of the lower crown. The reddish purple female flowers grow in whorls of two to five and are 10 to 12 mm (0.4 to 0.5 in) long. The pale yellow to yellowish orange male flowers are crowded clusters of catkins at the base of new shoots and are 8 to 14 mm (0.3 to 0.6 in) long. It is not uncommon to find a dominance of maleness or femaleness on individual trees.

Table 1—Time of pollen shedding in natural stands of lodgepole pine *(20,52*, modified)

Stand location	Elevation[1]		Years observed	Date of peak shedding
	m	*ft*		
Vancouver, BC	—	—	2	Middle to late May
Northwestern Washington	150	500	10	May 12
Mendocino White Plains, California	—	—	1	June 9
Northern Cascades	1200	4,000	—	Mid-June
Northern Idaho; western Montana	—	—	10	June 13
Central and eastern Washington and Oregon	790 to 1300	2,600 to 4,250	—	June 13
Southeastern Alberta (subalpine forest)	—	—	10	June 22
Sierra Nevada, California	1820	6,000	3	June 22
Central Montana; Yellowstone region	—	—	10	June 25
Northern Utah	2190	7,200	2	July 12
Southern Idaho	2070	6,800	1	July 7
Northern Idaho; western Montana	670 to 1265	2,200 to 4,150	10	June 6
Eastside Montana; Yellowstone National Park	975 to 2060	3,200 to 6,750	10	June 17

[1] Dash indicates data are not available

Pollen generally matures in mid-May to mid-July (table 1) *(20,52)*. The time at which pollen matures appears to be related to elevation and climate.

Seed cones usually mature in August, September, or October, more than a year after pollination. Inland forms and high elevation stands apparently mature earlier than coastal forms or low elevation stands. Cones open in early September in the Northern Rocky Mountains. Cone maturity is indicated by a change in color from purple-green to light brown *(54)*.

Seed Production and Dissemination— Lodgepole pine produces viable seed at an early age, commonly 5 to 10 years; germination percentage is as high as that of seed borne by mature trees. Pollen flowers have been observed on 2–0 seedlings in the Lucky Peak Nursery near Boise, ID.

Lodgepole pine is a prolific seed producer. Good crops can be expected at 1- to 3-year intervals, with light crops intervening. The cones withstand below freezing temperatures and are not generally affected by cone- and seed-feeding insects. Only squirrels and coreid bugs are significant seed predators. Seed production should not be taken for granted, however. Complete seed crop failures have occurred at 2800 m (9,200 ft) in northwest Wyoming for 2 to 4 years in a row *(42)*.

Cone production of individual dominant and codominant trees can vary from a few hundred to a few thousand per tree *(37)*. Cones are persistent, and serotinous (closed) cones accumulate for decades. Annual production may run from 173,000 to 790,000 seeds per hectare (70,000 to 320,000/acre) with half to one-third available for annual seedfall *(27)*. An annual seedfall of 99,000 to 222,000 seeds per hectare (40,000 to 90,000/acre) was found in central Montana *(58)*. These figures might be considered typical for interior lodgepole pine where some portion of the trees are of the serotinous type. In Oregon, where the nonserotinous cone habit is prevalent, seedfall ranged from about 35,000 to over 1.2 million/ha (14,000 to 500,000/acre) *(21)*. Most years seedfall was on the order of hundreds of thousands per hectare. Where stored seeds are in the millions per hectare (in closed cones), the number of seeds stored is probably 10 times that of seeds produced annually *(37)*.

Although the number of fully developed seeds per cone varies from as few as 1 to 2 to as many as 50, a normal average for large cone lots in the Rocky Mountains is from 10 to 24 seeds per cone *(42)*. Sierra Nevada populations range from 5 to 37 seeds per cone *(20)*.

The serotinous cone habit varies over wide geographic areas as well as locally *(37)*. Serotinous cones are not common in eastern Oregon, rare in coastal populations, and absent in the Sierra Nevada and southern California and Baja California populations *(20)*. Although common in the Rocky Mountains, this cone habit varies considerably *(37)*. Many stands in the Rockies have less than 50 percent serotinous-cone trees.

Lodgepole pine has long been regarded as a fire-maintained subclimax type. Its ability to regenerate in extremely dense stands to the exclusion of other species can be attributed to the closed cone habit. Millions of seeds per hectare are held in reserve for many years and are readily available to germinate on the seedbed prepared by fire. Recent evidence seems to indicate that fire selects strongly for the closed cone habit *(49)*.

Serotinous cones do not open at maturity because of a resinous bond between the cone scales. The bonds break with temperatures between 45° and 60° C (113° to 140° F) *(48)*, and cone scales are then free to open hygroscopically. Large quantities of seeds are thus available for regenerating a stand following fire. Closed cones at or near the soil surface (less than 30 cm or about 12 in) are also subjected to temperatures from insolation sufficient to open them and may provide seed in harvested areas. Some seeds may be damaged by fire, however, particularly in fires burning in logging slash.

Seeds stored in serotinous cones on the tree remain viable for years. Apparently, prolonged viability can be maintained so long as cones or seeds are not in contact with the ground. Once cones are on the ground, cones open. Damping-off fungi may infect the seed, rodents may feed on the seeds, or germination may occur; for the most part, seeds are not stored in the soil.

Lodgepole pine has relatively small seeds for pine. Seed weights vary considerably, ranging from 2.3 mg (0.04 grains) per seed in the Interior of Canada to 11.4 mg (0.18 grains) per seed in the Sierra Nevada *(20)*. Lodgepole pine seeds average about 298,000 cleaned seeds per kilogram (135,000/lb) for varieties *contorta*, 258,000/kg (117,000/lb) for *murrayana*, and 207,000/kg (94,000/lb) for *latifolia* *(54)*. Density of seedfall 20 m (66 ft) from the timber edge is only 10 to 30 percent of that at the timber edge for stands in the Rocky Mountains (fig. 2) *(42)*. Dispersal of sufficient seed to adequately restock an area often is only about 60 m (200 ft) *(23,38)*. Prevailing winds, thermal effects, or scudding on the snow may disperse seeds far beyond these distances, however.

The annual seedfall from nonserotinous cones helps in restocking relatively minor disturbances in the stand, in maintaining the presence of lodgepole pine in mixed stands, and in expanding conifers into

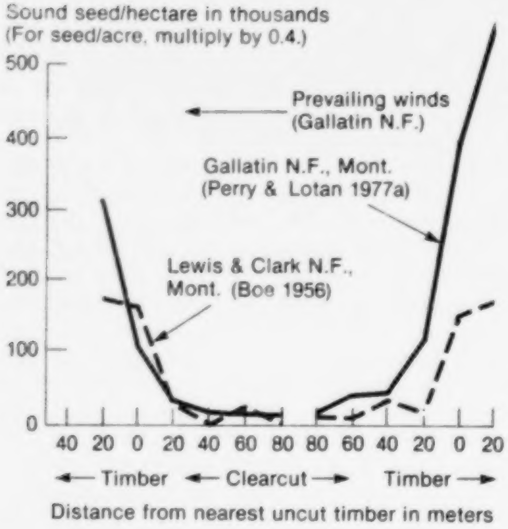

Figure 2—*Sound seed per hectare as a function of distance from the nearest timber edge.*

other vegetative types. Seldom do we find stands without some trees of the open-coned type. The efficacy of this seed source can be seen in the dense stands of lodgepole pine along road cuts, powerline rights-of-way, and ditches or where disturbance occurs near lodgepole pine stands (fig. 3).

Studies of seedfall have shown variation in the number of seeds released soon after cone maturation, but most seeds (80 to 90 percent) are released before the following growing season *(27)*.

Where large amounts of seed are stored in serotinous cones, a most effective means of seed dispersal in clearcuts is from cones attached to the slash and those knocked from the slash and scattered over the forest floor during slash disposal. Many cones on or near the ground are opened by normal summer soil surface temperatures *(35)*. In Montana 83 percent of the cones on the ground opened the first year on south slopes compared to 40 percent on north slopes. Maximum seed release from serotinous cones near the ground takes place during the first year of exposure. In fact, cones may open after the first few minutes of exposure to temperatures high enough to break the resinous bonds.

In slash, serotinous cones that are well above the ground behave like those on a tree—they remain closed, and stored seeds remain viable for years.

Seeds in unopened cones and those released from the slash may also be lost to rodents, fungi, and other destructive agents. Seeds from closed cones are usually available only for the first growing season following harvest, but stocking from open-cone seed sources can continue to increase for several years.

Slash disposal on areas where regeneration is planned from serotinous cones must be carefully planned and executed. Seed supply will be largely destroyed if slash to be burned is piled before cones have had a chance to open *(38)*. Piling slash should be delayed until sufficient cones have opened to assure adequate stocking. Piling then scatters seeds and opened cones and helps prepare the seedbed. Piling slash after germination can also decrease stocking because young seedlings are trampled or buried.

Broadcast burning may hasten release of seeds from cones not in a position to open from high soil-surface temperatures. Some seeds will be destroyed, however; the amount will vary with fire intensity.

Seedling Development—Germination under field conditions is good if climate and seedbed are favorable. Best germination occurs in full sunlight and on bare mineral soil or disturbed duff, free of competing vegetation. Germination is epigeal. Temperatures fluctuating between 8° and 26° C (47° and 78° F) favor germination. Adequate soil moisture is required for germination and survival during the critical few weeks following germination *(34,51,55)*. In southwest Montana and southeast Idaho, 75 to 90 percent of a season's total germination occurred

Figure 3—*Lodgepole pine regeneration in Colorado.*

during the 2 weeks following snowmelt in late June *(34)*, when the soil was saturated and temperatures were favorable. Germination can be delayed if cones do not open during the previous summer.

Although lodgepole pine germinates well on most organic seedbeds, such materials tend to dry faster than mineral soil and seedlings often die in this seedbed. Lodgepole pine seeds have little need for stratification and germination depends largely upon temperature *(20)*. At optimum temperatures and moisture, almost 100 percent of the seeds germinate rapidly.

Both shading and competition inhibit germination and survival. Newly germinated seedlings are relatively insensitive to temperature extremes. Because residual overstory following partial cutting usually does not provide the most favorable conditions for regeneration, clearcutting is generally recommended. On some areas, however, lodgepole pine has established itself in the shade of lightly cut or uneven-aged stands and may persist for many years in the understory. Some of these trees eventually may establish a crown sufficient to permit reasonable growth.

Drought is a common cause of mortality among first-year seedlings; losses vary with soil type and seedbed condition. Greatest losses occur on soils with low water-holding capacity, and duff and litter. Well decomposed organic material, incorporated in the soil, enhances seedling survival, however. Disturbed mineral soil seedbeds generally produce the best germination and survival *(34,40,41)*. Shading has been demonstrated to help under drought conditions in Wyoming *(10)*.

Drought losses usually decline considerably after the first growing season. First-year seedlings are particularly vulnerable because of a relatively shallow root system *(34,47)*.

Young, succulent seedlings may die because of high soil surface temperatures *(13)*. By 2 to 4 weeks of age, seedlings are able to withstand soil surface temperatures higher than 60° C (140° F), which commonly occur at high elevation sites. Freezing temperatures may kill seedlings either directly or by frost heaving. In much of the range of lodgepole pine, however, frosts occur regularly throughout the growing season and seedlings from different sources vary in frost resistance *(16)*. The amount of frost heaving varies considerably by soil type, location, and year of occurrence but can cause significant losses.

Lodgepole pine seedlings are poor competitors and competition from grass is often most detrimental. The Douglas-fir/pinegrass habitat type is one of the most difficult sites for lodgepole pine regeneration, particularly if the regeneration effort is delayed until a firm sod cover is established.

Grazing animals, particularly cattle, can cause seedling mortality by trampling. Sheep actually seek the succulent new "candles" in the spring and nibble needles and small branches if other feed is not abundant.

A common problem of regenerating lodgepole pine stands is overstocking, which results in stagnation at early ages. Many sites are stocked with tens of thousands and even hundreds of thousands of trees per hectare.

If trees are well distributed, stocking should not exceed 1,240 to 1,980 stems per hectare (500 to 800/acre) between 5 years and 20 years of age *(17)*. Proper distribution and full utilization of the site, however, may require establishment of 2,470/ha (1,000/acre) and thinning to obtain proper spacing. There is also potential for significant genetic gains from selection of elite trees when thinning.

An average height of 3.6 m (12 ft) and d.b.h. of 5 cm (2 in) on fully stocked 20-year-old stands was found on above average sites in Montana *(27)*. Average heights of 2.0 m (6.7 ft), 4.2 m (13.8 ft), and 7.6 m (24.9 ft) were found on low, medium, and high sites in 20-year-old stands in the Foothills Section of Alberta (for density class 1,240 stems per hectare or 500/acre at 70 years of age) *(32)*.

Lodgepole pine height growth begins earlier than any of its associates except other pines and larch *(53)*.

Vegetative Reproduction—Lodgepole pine can be grafted successfully, but results vary depending upon the clone *(20)*. Natural sprouting has been observed on the Bitterroot National Forest in Montana. Branches not severed often become leaders on stumps left in thinning operations.

Lodgepole pine cuttings are relatively easy to root. Adventitious roots have been developed artificially from 8-year-old lodgepole pine (by air-layering) after treatment with either indole-acetic or indole-butyric acid *(17)*.

Callus tissue cultures and liquid cell suspensions have been produced from seedling hypocotyl tissue, excised embryos, and actively growing shoots.

Sapling and Pole Stages to Maturity

Because lodgepole pine has little taper and thin bark it produces a higher volume of wood for a given diameter and height than many of its associates. Natural pruning is relatively poor, but limbs generally are of small diameter and lumber yields are good.

Table 2—Relationships among stand age and stocking level, and tree development and typical yield in natural stands of lodgepole pine, summarized for medium sites in Montana and Idaho (site index 22.9 m or 75 ft at base age 100 years)[1]

Age	Stocking		Average height of dominants		Average stand diameter		Total cubic volume		Merchantable volume		
yr	*trees/ha*	*trees/acre*	*m*	*ft*	*cm*	*in*	*m³/ha*	*ft³/acre*	*m³/ha*	*ft³/acre*	*fbm/acre*
20	1,240	500	5.5	18	8.6	3.4	16.1	230	—		
	19,770	8,000	3.0	10	4.1	1.6	28.0	400	—		
50	1,180	479	12.5	41	16.5	6.5	144.9	2,070	130.2	1,860	5,100
	15,200	6,150	9.1	30	6.9	2.7	165.9	2,370	—	—	—
80	1,030	418	18.0	59	20.6	8.1	285.6	4,080	266.0	3,800	12,100
	7,500	3,034	14.6	48	9.1	3.6	280.0	4,000	—	—	—
110	850	344	22.3	73	23.6	9.3	385.7	5,510	363.3	5,190	18,200
	4,600	1,861	18.9	62	11.4	4.5	357.0	5,100	273.0	3,900	8,400
140	680	275	25.3	83	26.7	10.5	448.7	6,410	426.3	6,090	23,200
	3,070	1,243	22.3	73	14.0	5.5	416.5	5,950	301.0	4,300	10,300

[1] Compiled from unpublished yield tables furnished by D. M. Cole, USDA Forest Service, Intermountain Research Station, Bozeman, MT. Cubic volumes are from trees 11.4 cm (4.5 in) in d.b.h. to a 7.6 cm (3 in) diameter top. Board foot volumes are from trees larger than 16.5 cm (6.5 in) in d.b.h. to a 15.2 cm (6 in) diameter top.

Growth and Yield—Growth and yield of lodgepole pine is greatly affected by stand density *(31)* (fig. 4) as well as by environmental factors *(2,6,22,46)*. In fact, site index curves have been developed with corrections for effects of stand density.

Maximum yield in the Rocky Mountains was 280 m³/ha (20,000 fbm/acre) at a density of 1,980 trees per hectare (800/acre), but only 21 m³/ha (1,500 fbm/acre) at a density of 4,450/ha (1,800/acre), assuming 5 fbm/ft³; original figures were in board feet *(27)*.

In extreme cases 70-year-old stands with 247,000 trees/ha (100,000 trees/acre) averaged only 1.2 m (4 ft) in height and less than 2.5 cm (1 in) in diameter at ground level.

Yields of 168 to 224 m³/ha (about 12,000 to 16,000 fbm/acre) can be found in old-growth Rocky Mountain lodgepole pine. Yields of more than 336 m³/ha (about 24,000 fbm/acre) are the result of a fortuitous combination of favorable initial stocking, good site quality, and absence of mountain pine beetle and dwarf mistletoe.

Relationships among age, stocking levels, and development in natural stands were summarized for medium sites in Montana and Idaho (site index 22.9 m or 75 ft at 100 years) (table 2). Under light to moderate stocking, live crowns are 25 to 60 percent of total height.

Mature sizes vary greatly between stands. In the Rocky Mountains, most trees at 140 years of age were 18 to 33 cm (about 7 to 13 in) in d.b.h. and 18 to 25 m (about 60 to 80 ft) in height *(27)*.

Trees in the Blue Mountains of Oregon average 30 cm (about 12 in) in d.b.h. and 23 m (about 75 ft) tall at 100 years of age. Sierra Nevada trees the same age are larger, averaging 42 cm (about 16 to 17 in) in d.b.h. and 28 to 30 m (about 90 to 100 ft) tall. Coastal trees are smaller but vary greatly. Mature trees range from 15 to 50 cm (about 6 to 20 in) in d.b.h. and only 6 to 12 m (20 to 40 ft) tall. Dwarf lodgepole pines are only about a meter (2 to 5 ft) tall and are found along the coast in Mendocino County, CA. This small size is thought to be caused by a highly acid hardpan.

Growth of lodgepole pine is often so stagnant that stand culture is not practical. Early management and control of stocking greatly affects growth and yield of lodgepole pine stands *(17)*. Average annual growth in old-growth unmanaged stands in the central Rocky Mountains only was 0.4 to 0.6 m³/ha (about 25 to 40 fbm/acre) because of large numbers of small trees and a high incidence of dwarf mistletoe

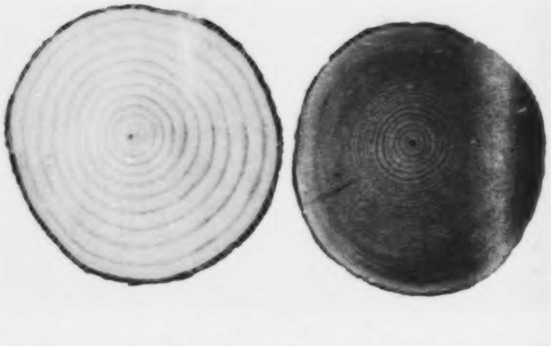

Figure 4—*Spacing greatly affects lodgepole pine diameter growth. Section on left comes from a 17-year-old tree; the one on the right, a 117-year-old tree, Cherry Creek, Gallatin National Forest, MT.*

(4). (Calculations assume 5 fbm/ft^3; original figures were in board feet). Annual net growth may be increased to 2.1 to 5.6 m^3/ha (about 150 to 400 fbm/acre) by controlling stand density and reducing dwarf mistletoe infection *(5,25)*.

Control of stand density offers the greatest opportunity for increasing productivity of any readily available management practice (table 2).

Culmination of total cubic volume occurs as early as 40 years in severely stagnated stands, and between 50 and 80 years for overstocked, but not greatly stagnated, stands. Merchantable volume culmination in stands of the latter type occurs between 110 and 140 years, depending on merchantability standards.

Thinning of young overstocked and stagnating stands can restore growth potential and redirect it into merchantable-size products. With more complete utilization (lower merchantable d.b.h. and top diameters), most of the yield increase possible from thinning is attained with the first entry, a stocking control thinning *(17)*.

Rooting Habit—The root system of lodgepole pine varies considerably in form, depending on soil type. Root growth is particularly important during the critical first year. Root growth of 12.7 to 15.2 cm (5 to 6 in) was reported for seedlings growing on prepared seedbeds in Montana and Idaho *(34)*. First-season seedlings had an average root depth of only 9.6 cm (3.8 in) on scarified, unshaded seedbeds in the central Rocky Mountains *(47)*. Seedlings growing near grass competition usually do not penetrate beyond 5 or 6 cm (about 2 in).

Taproots and vertical sinkers are common, but where a hardpan or water table is encountered, the taproot may die, bend, or assume a horizontal position. Planting may affect root configuration. Taproots of seedlings planted with "J–roots" often grow horizontally for many years before sinkers develop.

Because of its shallow root system, lodgepole pine is susceptible to windfall, particularly after stands are opened by harvesting. Windfirmness varies with stand density, soil conditions and topography. Shallow roots are common above hardpan or in shallow, rocky soils.

Reaction to Competition—Lodgepole pine is very intolerant of shade and competition from other plant species. Occasionally seedlings become established under a forest canopy, but these individuals rarely do well. In spite of its shade intolerance, lodgepole pine maintains itself in dense stands for long periods, often for 100 years or more.

In the absence of fire, lodgepole pine is usually succeeded by its more tolerant associates, such as Engelmann spruce and subalpine fir. Succession proceeds at variable rates, however, and is particularly slow in some high elevation forests.

Pure stands of lodgepole pine persist for varying lengths of time. In northern Idaho and central Oregon, stands begin to break up at 80 to 100 years, while stands at higher elevations, such as in Montana, southern Idaho, Utah, and Wyoming, last for several hundred years. Pure stands in and around Yellowstone National Park contain 300- to 400-year-old trees, with several groups of younger even-aged trees. These stands no doubt originated as even-aged stands but have been breaking up for more than two centuries.

The ability of lodgepole pine to regenerate at the expense of other species is due not only to cone serotiny but also to seed viability, germinative energy, early rapid growth, and ability to survive a wide variety of microsite and soil situations *(39)*.

Compared to its associates, lodgepole pine is intermediate in its needs for water, requiring more than Douglas-fir and ponderosa pine and less than Engelmann spruce and subalpine fir. On some sites, lodgepole pine appears to compete well for water, however, and grows where other species may be excluded because of lack of water *(45,57)*; on others it appears to be tolerant of high water tables *(14,43)*. It is also intermediate in its tolerance to extremes of temperature *(27)*.

Lodgepole pine shows good response to thinning at an early age (fig. 5) *(17)*. Heavily stocked stands must be thinned before stagnation occurs. The best age for thinning varies with site and density. Poor sites and overstocked stands particularly must be thinned as early as age 10.

Diameter growth acceleration is usually greatest in heavy thinnings; cubic volume and basal area growth are usually greatest in light thinnings *(27)*. Although mechanical thinning, as with bulldozer strips, is a convenient alternative, obtaining a proper response *(36)* is difficult.

At older ages, growth response is strongly correlated with crown size, vigor, and amount of release provided *(27)*. Attempts at partial cutting of mature and over-mature stands have resulted in little gain or even negative net volume growth *(1,28)*.

Lodgepole pine can be maintained best in a vigorous, productive forest by using a silvicultural method that regenerates even-aged stands *(38)*. This often may be accomplished by clearcutting (fig. 6) and by relying upon natural regeneration or planting. Planting provides an excellent opportunity for initial stocking control and/or genetic improvement.

Damaging Agents—The mountain pine beetle *(Dendroctonus ponderosae)* is the most severe insect pest of lodgepole pine. The epidemics that periodically occur in many lodgepole pine stands seriously affect the sustained yield and regulation of managed stands.

Adult beetles attack lodgepole pine in July or August, introducing bluestain fungi *(8)*. The beetles construct egg galleries in the phloem where larvae feed and together with the fungi, girdle and kill the tree. Larvae overwinter in the tree, complete development, and emerge as adult beetles in the spring.

Harvesting has been considered as a means of preventing mountain pine beetle epidemics *(19)*. Silvicultural practices in an integrated program for controlling losses to mountain pine beetle have been suggested *(9,18)*. No mortality occurred in heavily thinned stands in Oregon where vigor ratings were high *(44)*.

The mountain pine beetle has played an historic role in the dynamics of lodgepole pine ecosystems. By periodically invading stands and creating large amounts of fuels, which are eventually consumed by fire, creating favorable conditions for regeneration *(12,39)*, the beetle has increased the probability that lodgepole pine will reoccupy the site at the expense of other species.

Another aggressive bark beetle that attacks lodgepole pine is the pine engraver *(Ips pini)*. Ips commonly develops in logging slash, especially slash that is shaded and does not dry quickly. Prompt slash disposal is an effective control measure. Ips also can build up in windthrows.

Other insects that can be damaging local pests are the lodgepole terminal weevil *(Pissodes terminalis)*, which can be destructive to elongating terminal leaders; larvae of the Warren's collar weevil *(Hylobius warreni)*, which girdles roots and the root collar; larvae of the weevil *Magdalis gentilis*, which mine branches; various sucking insects, such as the pine needle scale *(Chionaspis pinifoliae)*, the black pineleaf scale *(Nuculaspis californica)*, and the spruce spider mite *(Oligonychus ununguis)*; and several defoliating insects, among which are the lodgepole sawfly *(Neodiprion burkei)*, the lodgepole needle miner *(Coleotechnites milleri)*, the sugar pine tortrix *(Choristoneura lambertiana)*, the pine tube moth *(Argyrotaenia pinatubana)*, and the pandora moth *(Coloradia pandora)* *(7)*.

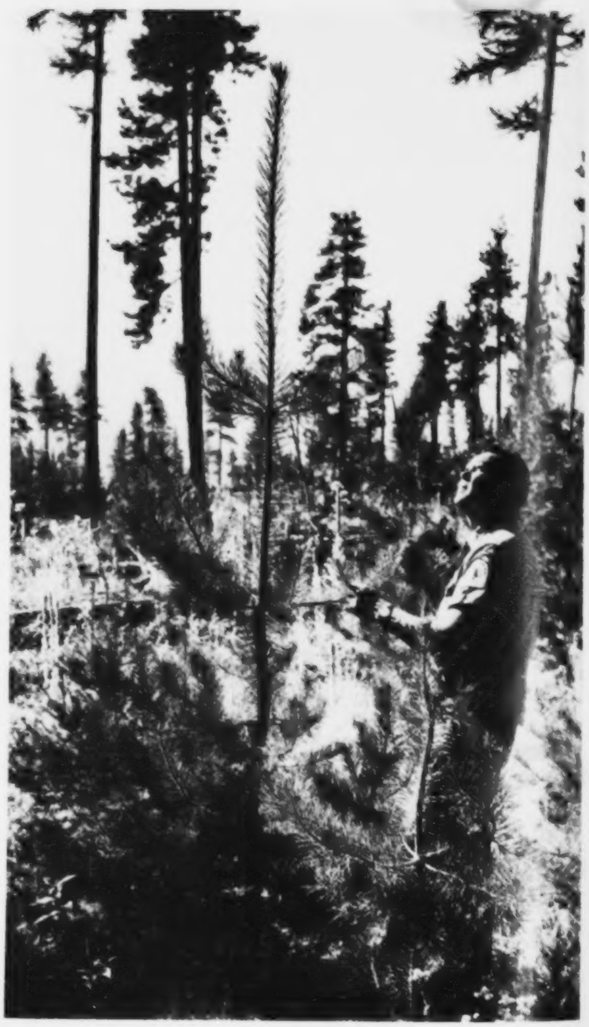

Figure 5—*With adequate spacing early growth of lodgepole pine is rapid. This lodgepole pine grew 102 cm (40 in) in 1 year, Scalp Mountain, Kootenai National Forest, MT.*

Dwarf mistletoe (particularly *Arceuthobium americanum*) is the most widespread and serious parasite affecting lodgepole pine *(11,29)*. *A. americanum* seeds are forcibly ejected from the fruit for distances as great as 9 m (about 30 ft). The sticky seeds adhere to the foliage of potential host trees. The proportion of trees visibly infected can double each 5 years between the ages of 10 and 25, with nearly a third of the trees infected at age 25 *(29)*.

Rate of spread in young stands is about 0.3 to 0.5 m (1.0 to 1.5 ft) per year, with the fastest rate in dense stands. In many areas, more than 50 percent of lodgepole pine forests are infected. Dwarf mistletoe infection results in reduced diameter and height growth, increased mortality, reduced wood quality, decreased seed production, and overall decreased vigor.

Both harvesting and fire can greatly lessen the rate of spread and rates of infection. Effective control can be accomplished by clearcutting and locating boundaries of the unit to minimize reinfection from surrounding stands. Fire can effectively limit spread of dwarf mistletoe by eliminating sources of infection and establishing vast acreages of dwarf mistletoe-free areas.

Lodgepole pine is subject to attack by many fungal pathogens *(33)*. These fungi are responsible for reduced growth and considerable cull and mortality. They also contribute in no small measure to the large amounts of logging residues that commonly occur when lodgepole pine is harvested.

One of the most serious diseases in lodgepole pine is a stem canker caused by *Atropellis piniphila*. Cankered stems are usually useless for lumber or posts and poles. Stem cankers of rust fungi cause extensive mortality, growth loss, and cull in lodgepole pine. Of these comandra blister rust *(Cronartium comandrae)* is the most serious. The western gall rust *(Peridermium harknessii)* is especially damaging; trunk cankers can cause cull in logs and can kill seedlings and saplings. Because this rust does not require an alternate host, it can directly reinfect pines. Other fungi attack lodgepole pine and may cause serious losses in wood production. Examples are needle casts (such as *Elytroderma deformans* and *Lophodermella concolor*); root rots (such as *Armillaria mellea* and *Heterobasidion annosum*); and wood decays (such as *Phellinus pini* and *Peniophora pseudo-pini*).

Seed and seedling diseases are not usually damaging, although locally several mold fungi are as-

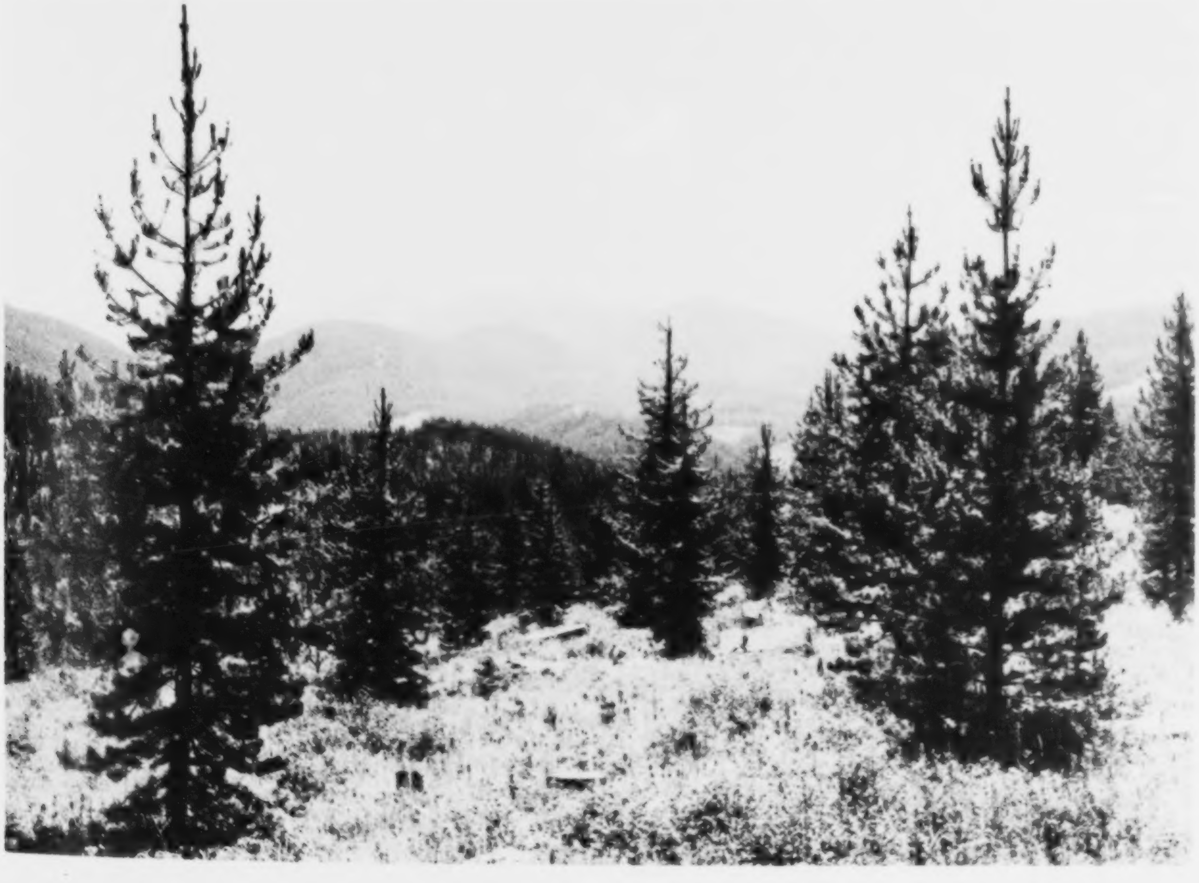

Figure 6—*A 20-year-old lodgepole pine clearcut in Moser Creek, Gallatin National Forest, MT.*

sociated with seed losses in germination, and rotting and damping-off can affect young seedlings.

Because of its relatively thin bark, lodgepole pine is more susceptible to fire than Douglas-fir and many other associates. It is less susceptible than Engelmann spruce or subalpine fir. Mortality from beetle epidemics often creates large amounts of jackstrawed fuel, which ignites easily from lightning and other sources and hampers fire control efforts.

Chinook winds following extremely cold weather occasionally cause red belt injury, particularly in Canada and Montana. Defoliation of trees is common and mortality can occur over large areas. Heavy snow can break or bend trees, particularly in dense stands with narrow crowns and intense root competition. Thinning can contribute to snow breakage, particularly if previously dense stands are opened suddenly.

Animals can cause considerable damage in thinned stands in some areas. Porcupines were attracted to thinned and fertilized stands in Montana. Pocket gophers often cover small seedlings under their entrance mounds and "winter-casts." They also feed on or clip both roots and tops. Gopher populations often explode as vegetation increases in open areas.

Special Uses

Lodgepole pine is not only an important timber species but is also a major tree cover in many scenic and recreational areas and on critical watersheds. It provides many acres of wildlife habitat and is associated with many grazing allotments throughout its range. It is important to local communities throughout the West.

Lodgepole pine is used for framing, paneling, posts, corral poles, utility poles, railroad ties, and pulpwood. As new developments such as structural particleboard become practical, the rapid juvenile growth of the species will be an advantage where gross cubic volume becomes important. Even now, with properly designed machinery, it is economically harvested, and this harvesting, properly done, can enhance watershed, forage, wildlife habitat, and scenic and recreational values.

Genetics

This summary is based on a recent review of the literature on the genetics of lodgepole pine *(20)*. The ability of some strains of lodgepole pine to grow well on poor sites and in cold climates has interested European foresters for many years. Much of what is known about the genetic diversity of the species has been learned from provenance tests, mostly in northwestern Europe. These tests have established that much of the variation observed in natural stands of lodgepole pine has a genetic basis.

Population Differences

Lodgepole pine has evolved several highly differentiated but inter-fertile geographic races that differ morphologically and ecologically:

Rocky Mountain–Intermountain Race (var. *latifolia*)—Within the extensive range of this race, the trees are relatively tall, the bark is usually thin, and the needles are long and moderately wide. Cones are produced regularly from an early age and often are serotinous. The trees are intolerant and stands are considered seral in most forest communities. The persistent cones are hard and heavy, with protuberant scales. The cones may be reflexed, projecting, or semierect on the branch. Semierect cones, common only in this race of lodgepole pine, also are common in the closely related jack pine *(Pinus banksiana)*, which overlaps and hybridizes with lodgepole pine in parts of western Canada. Semierect cones are present in some lodgepole stands remote from the region of overlap and may indicate earlier contacts between the two species during the Ice Age. Seeds are small, highly dispersable, retain their viability for many years in serotinous cones, and germinate rapidly without pretreatment. Seedlings have few cotyledons and juvenile growth is rapid. Local variations include a high frequency of three-needled fascicles in the Yukon, a possible Ice Age refugium of lodgepole pine, and (in stands in southern interior British Columbia and adjacent United States) the variable occurrence of thick bark, repeated stem forking, unusually fast juvenile growth, a low incidence of serotinous cones, or a high incidence of semierect cones.

Sierra–Cascade Race (var. *murrayana*)—In its typical form (in the Sierra Nevada and other California mountains), this is the most distinctive race of lodgepole pine, but it intergrades with var. *latifolia* in the central and northern Cascades. It is inherently slow-growing in height, but diameter growth is more sustained than in other races. The trees have thin bark and reach much greater diameter—and probably greater ages—than elsewhere in the range of lodgepole pine. This race appears to have a stable ecological role and distribution that is not closely related to fire. The relatively short needles are the widest in the species. Seeds are by far the largest, and seedlings have more cotyledons than those of other races. Cones are lightweight and projecting or reflexed, with flattish scales. The cones open promptly at maturity and do not persist on the tree for long periods.

Coastal Race (var. *contorta*)—The thick-barked trees are relatively small, short-lived, and inherently branchy. Now mostly confined to marginal sites (muskegs, dunes, serpentine soils, rocky sites), this race pioneered forest succession in the Pacific Coast region at the end of the Ice Age. Needles are short, rather narrow, and have more stomata per unit area than the leaves of inland races. Flowering is abundant, and female strobili tend to mature earlier than the male. The cones are reflexed and persistent. Cones usually open not long after they mature, but serotiny is increasingly common toward the interior. Seeds are small to medium-sized, and germination is slower than that of the interior races. Early height growth nearly always is faster than that of inland populations at the same latitude. Local variations include a chemically distinctive northern muskeg ecotype extending south to western Washington.

Mendocino White Plains Race (var. *bolanderi*)—This race, restricted to a narrow strip of highly acid podsol soils paralleling the coast of Mendocino County, CA, is probably an edaphic ecotype derived from the contiguous coastal race. Trees are dwarfed in nature but not when planted on other sites. Female strobili mature earlier than the males. Trees are extremely heavy pollen producers, and compared to coastal trees they produce high ratios of male to female strobili. The needles are short, narrow, and lacking in resin canals. Cones are reflexed, heavy, knobby, and often serotinous.

Del Norte Race (not named)—This poorly known race has a limited distribution on serpentine and other ultramafic soils in the low coastal mountains of Del Norte County, northwestern California. Cones are heavier and more reflexed than those of any other race and often are serotinous. This group is geographically isolated from the others, but the composition of its cortex resin suggests that it may be an offshoot of the coastal race.

Hybrids

No significant genetic barriers have been encountered in artificial crosses between geographical races of lodgepole pine. The species has been successfully crossed with jack pine and Virginia pine (*Pinus virginiana*). Crossability with jack pine is moderately high, and natural hybrids are common where their ranges overlap. Lodgepole × jack pine hybrids are fertile, but pollen abortion sometimes is high. Sierra Nevada lodgepole × jack pine hybrids are poorly adapted to jack pine's range. Artificial lodgepole × Virginia pine hybrids are difficult to produce, and most are chlorotic and dwarfed.

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Pinus echinata Mill. Shortleaf Pine

Pinaceae Pine family

Edwin R. Lawson

Shortleaf pine (*Pinus echinata*) is one of the four most important commercial conifers in the southeastern United States. Depending upon locale, the species is also called shortleaf yellow, southern yellow, oldfield, shortstraw, or Arkansas soft pine. Shortleaf pine tolerates a wide range of soil and site conditions and maintains its growth rate for a relatively long period. However, the species tends to grow slower during the early years after establishment than other southern pines. Shortleaf pine is the most common species regenerated in the northern and western parts of its range.

Habitat

Native Range

Shortleaf pine (fig. 1) has the widest range of any pine in the southeastern United States. It grows in 22 States over more than 1 139 600 km² (440,000

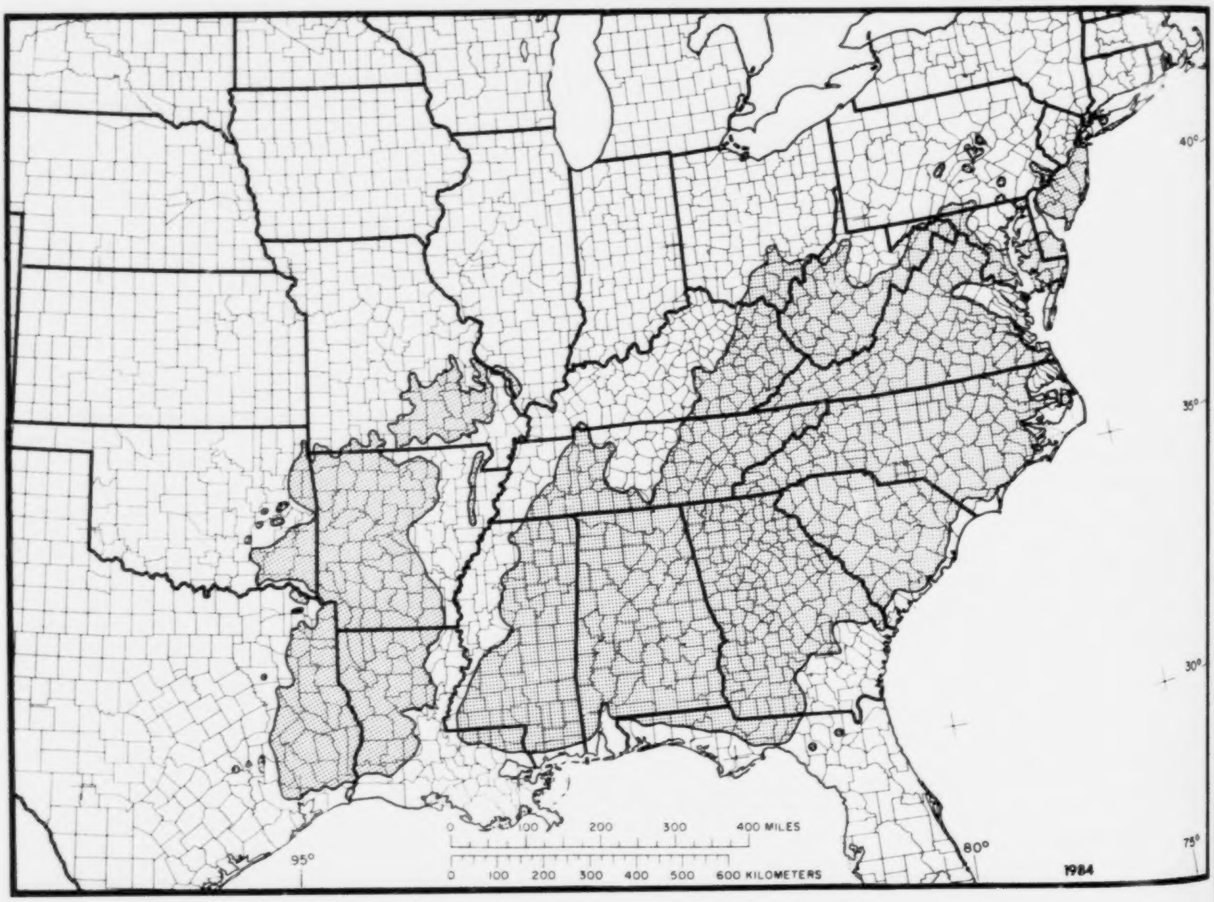

Figure 1—*The native range of shortleaf pine.*

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mi²), from southeastern New York and New Jersey west to Pennsylvania, southern Ohio, Kentucky, southwestern Illinois, and southern Missouri; south to eastern Oklahoma and eastern Texas; and east to northern Florida and northeast through the Atlantic Coast States to Delaware *(33).* In 1915, shortleaf pine was reported to grow in 24 States. Fossil pollen found in Michigan suggests that it may have once grown there *(18).*

Climate

Shortleaf pine grows in a fairly humid region but is the least exacting of the southern pines as to temperature and moisture *(18).* Annual precipitation averages between 1020 mm (40 in) on the western edge of its range and 1520 mm (60 in) at the southern tip of its range *(59).* Snowfall averages less than 41 cm (16 in) over most of the shortleaf pine range but may be twice that amount in some of the higher elevations of the Appalachians northward into Pennsylvania. The region of best development for the species is in Arkansas, northern Louisiana, and the southern Piedmont, where precipitatin ranges from 1140 to 1400 mm (45 to 55 in) and averages 1270 mm (50 in). The 10° C (50° F) average annual temperature isoline closely parallels the northern limit of shortleaf pine. Over its range, average annual temperatures vary from 9° C (48° F) in New Jersey to 21° C (70° F) in southeast Texas.

Soils and Topography

Shortleaf pine's adaptability to a great variety of site and soil conditions partly accounts for its wide distribution. The best growth rate is on South Atlantic and Gulf Coastal Plain soils. However, most of the soils that shortleaf pine occupies are classed in the order Ultisols and suborder Udults. Soils in this suborder are usually moist and relatively low in organic matter in subsurface horizons. They are formed in humid climates that have short or few dry periods during the year. Two great soil groups, Paleudults and Hapludults, include the primary soils occupied by shortleaf pine. Paleudults have a thick horizon of clay accumulation without appreciable weatherable materials. Hapludults may have either relatively thin clay subsurface horizons or a subsurface horizon with appreciable weatherable materials, or both. Shortleaf pine may occupy soils in other orders, but they do not constitute a significant part of its range *(58).*

Shortleaf pine grows best on deep, well-drained soils having fine sandy loam or silty loam textures. These soils are found primarily on flood plains. Site indices for shortleaf pine on these sites may exceed 30 m (100 ft). Very shallow, rocky soils on upland sites in the lower rainfall sections of the species' range have very low site indices, sometimes as low as 10 m (33 ft) *(21).* In the upland areas of its range, site indices at base age 50 years for natural stands average between 15 m (50 ft) and 23 m (75 ft) *(20,25).* In north Mississippi, site indices of sample plots ranged from 6 m (20 ft) to 30 m (97 ft) for shortleaf pine plantations varying in age from 17 to 29 years *(69).*

Shortleaf pine does not grow well on soils with a high calcium content, high pH, or excessive internal drainage. It is also reported to be more abundant than loblolly pine on the drier, better drained, and less fertile soils in the Piedmont. The difference is partly attributable to shortleaf pine's larger root system, lower tolerance to poor soil aeration, and lower demand for nutrients *(18).*

Shortleaf pine grows at elevations as low as 3 m (10 ft) in southern New Jersey and up to 910 m (3,000 ft) in the Appalachian Mountains. It grows up to 300 m (1,000 ft) in Pennsylvania. Its best development is attained at elevations of 180 m (600 ft) to 460 m (1,500 ft) in the Piedmont and 45 m (150 ft) to 350 m (1,150 ft) in Louisiana and Arkansas, although it grows at elevations up to 610 m (2,000 ft) in Arkansas, Missouri, and Oklahoma *(16,18).*

Associated Forest Cover

Shortleaf pine is now considered a major component of three forest cover types (Society of American Foresters, *16*), Shortleaf Pine (Type 75), Shortleaf Pine–Oak (Type 76), and Loblolly Pine–Shortleaf Pine (Type 80). Although shortleaf pine grows very well on good sites, it is genearlly only temporary and gives way to more competitive species, particularly hardwoods. It is more competitive on drier sites with thin, rocky, and nutrient deficient soils. With the species' ability to grow on the medium and poor sites, it is not surprising that shortleaf pine is a minor component of at least 15 other forest cover types.

21	Eastern White Pine
40	Post Oak–Blackjack Oak
43	Bear Oak
44	Chestnut Oak
45	Pitch Pine
46	Eastern Redcedar
51	White Pine–Chestnut Oak
52	White Oak–Black Oak–Northern Red Oak
57	Yellow-Popular
70	Longleaf Pine
78	Virginia Pine–Oak

79	Virginia Pine
81	Loblolly Pine
82	Loblolly Pine–Hardwood
110	Black Oak

In addition to species in the cover types, other common associates include scarlet oak *(Quercus coccinea)*, southern red oak *(Q. falcata)*, blackgum *(Nyssa sylvatica)*, sweetgum *(Liquidambar styraciflua)*, Table Mountain pine *(Pinus pungens)*, mockernut and pignut hickories *(Carya tomentosa* and *C. glabra)*, winged elm *(Ulmus alata)*, sourwood *(Oxydendrum arboreum)*, red maple *(Acer rubrum)*, water oak *(Quercus nigra)*, willow oak *(Q. phellos)*, American beech *(Fagus grandifolia)*, and Carolina ash *(Fraxinus caroliniana)*. Common understory woody plants include mountainlaurel *(Kalmia latifolia)*, flowering dogwood *(Cornus florida)*, redbud *(Cercis canadensis)*, persimmon *(Diospyros virginiana)*, and eastern redcedar *(Juniperus virginiana)*.

Among the more common understory shrubs, vines, and herbaceous vegetation are blueberries *(Vaccinium* spp.), huckleberries *(Gaylussacia* spp.), deerberry *(Vaccinium stamineum)*, Japanese honeysuckle *(Lonicera japonica)*, greenbriers *(Smilax* spp.), Virginia creeper *(Parthenocissus quinquefolia)*, poison ivy *(Toxicodendron radicans)*, grape *(Vitis* spp.), asters *(Aster* spp., tick-trefoil *(Desmodium* spp.), tickseed *(Coreopsis* spp.), bushclover *(Lespedeza* spp.), St. Andrews cross *(Ascyrum hypericoides* var. *multicaule)*, birdfoot violet *(Viola pedata)*, sensitive brier *(Schrankia* spp.), early azalea *(Rhododendron roseum)*, pussytoes *(Antennaria* spp.), butterfly-pea *(Clitoria mariana)*, senna *(Cassia* spp.), bugbanes *(Cimicifuga* spp.), longleaf uniola *(Uniola longifolia)*, panicums *(Panicum* spp.), sedges *(Carex* spp.), and bluestems *(Andropogon* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Shortleaf pine is monoecious *(29)*. Male and female strobili emerge from late March in the southwestern part of its range to late April in the northeastern sections. Open-grown trees may produce strobili 2 weeks earlier *(18)*. Male strobili are more common on the basal part of new shoots, mostly on older lateral branches in the lower crown. The male strobili are arranged in indistinct spirals in clusters 1.3 to 5.1 cm (0.5 to 2.0 in) long. They may be green or yellow to reddish purple before ripening but become brown to light brown at the time of pollen shed. Female strobili emerge from the winter bud soon after the male strobili and are green or red to purple. They are nearly erect at the time of pollination, and 1.0 to 3.8 cm (0.4 to 1.5 in) long. After pollination, scales of the female strobili close and slow development begins. By the end of the first growing season they are about one-eighth to one-fifth the length of mature cones. Cones develop rapidly after fertilization takes place in early spring or summer of the second growing season. They mature by late summer or early fall and are green to light or dull brown when ripe *(29)*.

Shortleaf pine generally does not bear seeds until about 20 years of age, but both male and female flowers have been reported on 5-year-old trees. Viable seeds have been produced on 9-year-old trees, although this is exceptional. Trees usually produce seeds abundantly when they reach a diameter of about 30 cm (12 in) *(18)*.

Seed Production and Dissemination—Seedfall usually begins in late October or early November when cones reach a specific gravity of about 0.88 or when they will float in SAE 20 motor oil *(60)*. As the cones dry, the bracts open, allowing the winged seeds to fall out. Most seeds fall fairly close to the tree from which they originate, but in varying patterns. In an Arkansas study, half of the shortleaf pine seeds fell into a forest clearing within 20 m (66 ft) of forest walls 21 m (70 ft) high, and 85 pecent fell within 50 m (165 ft) of the forest walls *(71)*. Wall height and orientation and prevailing wind direction had little effect on the dispersal pattern, probably because of topographic features and frontal winds. In other observations, however, where prevailing winds were from one direction during seedfall, seeds were dispersed in a v-shaped pattern with the apex at the base of the tree. Under such conditions, several times as many seeds were caught in traps at a distance of 40 m (132 ft) from the tree on the leeward side as were caught at a distance of 20 m (66 ft) on the windward side *(18)*.

About 70 percent of the seeds fall within a month after maturity and 90 percent within 2 months. Some seeds continue to fall into April, and cones persist on the tree long after they are empty *(18,71)*.

Shortleaf pine cones yield about 25 to 38 full seeds each *(18,72)* or about 0.9 to 1.4 kg (2 to 3 lb) of seeds per 45 kg (100 lb) of cones. The number of cleaned seeds per kilogram ranges from 70,800 to 160,700 (32,100 to 72,900 per pound) and averages 102,100 (46,300) *(29)*. The number of seeds produced per tree and number of seeds per cone can be significantly increased by releasing seed trees from competition *(71)*, although the number of seeds per cone may not always increase *(43)*. The average number of cones per tree for unreleased trees was 498 compared with 1,069 for those released from competition *(72)*. Releasing seed trees by removing hardwoods and thinning from below to densities at least as low as 11.5 m²/ha (50 ft²/acre) greatly increases seed production in shortleaf pine stands *(43)*.

Good to excellent cone crops occur every 3 to 10 years in the Northeast and 3 to 6 years in the South *(18)*. In the Georgia Piedmont, seed crops were most frequent in the northern portions *(6)*. Shortleaf pine seed production was studied in natural stands in Oklahoma, Arkansas, and Missouri during a 10-year period from 1965 through 1974 *(57)*. The lowest production was 4,900 sound seeds per hectare (2,000/acre) and the highest was 1,845,800/ha (747,000/acre). Seed yields of at least 66,700/ha (27,000/acre) occurred in 7 of the 10 years, and no consecutive 2-year periods had less than 79,100/ha (32,000/acre). In another study *(72)*, the lowest seed production from 25 trees per hectare (10/acre) for three consecutive 3-year periods was 761,100/ha (308,000/acre).

Seedling Development — Shortleaf pine seeds that lie on the ground during the winter are naturally stratified and epigeous germination takes place in early spring. There is some evidence that a few seeds do not germinate until the second year, but this phenomenon has not been verified. Many seeds are eaten by birds and small mammals, and only a few actually germinate and produce seedlings. Seedbed treatments that expose mineral soil tend to increase the initial establishment of seedlings *(4,18,31,73)*. Scarification during logging and burning provide effective site preparation for natural regeneration of shortleaf pine. Control of hardwood competition is also necessary to insure survival of seedlings, although some residual hardwoods have the beneficial effect of shading and protecting them from drying winds, especially on southerly aspects during the first few years after establishment. Generally, about 100 sound seeds are required to establish each seedling, although this number varies considerably depending on seedbed condition, seed year, and environmental factors *(73)*.

Shortleaf pine seedlings may also be established by direct seeding, the success of which depends on suitability of sites and seedbeds, protection of seeds from birds and rodents, amount of seeds and timing of sowing, and control of competition. Suitable seedbeds are obtainable by mechanical site preparation, such as mowing, disking, shearing and raking, roller drum chopping, ripping, prescribed burning, chemical treatments, or hand methods, such as kicking or raking off litter. Combinations of these techniques are often used to provide the most effective site preparation *(4,47)*.

It is necessary to select good quality seeds that have been properly collected, stored, stratified, and treated with bird and rodent repellents. Seedlots should have 95 percent purity and at least 80 percent germinative capacity *(4)*. Even properly stratified seed should be treated with repellents *(13)*. Seeding at two or three times the normal rate has been done, but this is an expensive and risky way to combat seed depredation *(47)*.

For broadcast seeding, a rate of about 0.56 kg/ha (0.5 lb/acre) is recommended, although about half this amount is adequate for well-prepared seedbeds *(13)*. For spot seeding, three to five seeds should be dropped on each spot. Row seeding requires single seeds spaced about 30 cm (12 in) apart along the row, furrow, or line *(4)*. It is better to sow at relatively high rates initially with any seeding method, then adjust rates for the local conditions as experience dictates *(47)*. Both natural seedfall and direct seeding have the disadvantage of high variability in achieved stocking levels, although these methods are generally much less expensive to apply.

Shortleaf pine seedlings are commonly produced in nurseries and outplanted as 1-year-old, bare-rooted nursery stock. Seeds are usually stratified for about 60 days at 1° to 5° C (34° to 41° F), sown in the spring at the rate of 430/m² (40/ft²), pressed into the soil, and mulched with burlap or chopped pine needles *(29)*. Seedling densities as low as 270/m² (25/ft²) are currently being considered with other nursery practice modifications to provide seedlings that will have better survival and growth *(4)*. Nursery-grown seedlings develop rapidly and are ready for lifting and outplanting by late fall. Occasionally, seedlings are grown to larger sizes for planting on difficult sites or for special purposes. Care must be taken to insure proper lifting, handling, and storage of seedlings throughout the entire planting process. The safest time to plant the seedlings is from late February to early March, after most of the severe weather has passed. Planting in April or May is not recommended because seedlings may be lost to drought and severe competition from established vegetation. Seedlings are currently being planted at spacings of 2.4 x 2.4 m (8 x 8 ft) to 3.0 x 3.0 m (10 x 10 ft), which provide 1,683 to 1,077 seedlings per hectare (681 to 436 per acre), respectively *(4)*.

Planting of containerized seedlings generally allows more efficient use of seed, provides better survival and faster initial growth, and extends the planting season. Depending on the type of container, the seedling may be either planted with the container or removed before planting *(2,3,46)*.

Shortleaf pine seedlings develop a persistent J-shaped crook near the ground surface at 2 to 3 months of age. The stem is usually prostrate as shoot growth begins but subsequently turns upward, forming the crook. Axillary and other buds form near the crook and initiate growth if the upper stem is killed by fire or is severed *(18)*.

Shortleaf pine seedlings grow slowly as the root system develops during the first year or two after establishment. The developing seedlings and saplings attain most of their height growth early in the growing season, usually by early July *(18)*. Shortleaf pines show growth response to late-season rainfall, however, if it is sufficient to replenish soil water. Average annual height growth during the sapling stage ranges between 0.3 and 0.9 m (1 and 3 ft) depending on locality and site conditions *(18,36,53,69)*.

Competition from woody plants *(35)* and nonwoody plants *(15)* is highly detrimental to growth and development of shortleaf pine seedlings and saplings *(8,31,47)*. Preharvest hardwood control by stem injection, soil application of herbicide, and rotary mowing with herbicide spraying facilitated establishment of loblolly and shortleaf pine natural regeneration in a 75- to 80-year-old stand in southern Arkansas. After 3 years, the hardwood control treatments provided optimum pine seedling stocking and significantly taller pine seedlings than the plots without hardwood control *(8)*. Ripping of soils on eroded, compacted, or rocky sites followed by planting in the rips has improved performance of seedlings *(4)*. Elimination of overstory competition resulted in 60-percent survival of 5-year-old trees compared with 16 percent where the overstory remained. Heights of the tallest seedlings at age 5 were 18 cm (7 in) on the untreated and 122 cm (48 in) on the treated area *(18)*. On the Cumberland Plateau, shortleaf pine seedlings that were suppressed for 2 years after underplanting in a low-grade hardwood stand resumed good growth after the overstory was killed, but a year's height growth was lost for each year of deferred release *(47)*.

Vegetative Reproduction—Shortleaf pine can be vegetatively propagated by either rooting or grafting of scions, but techniques for production of new plants from parts such as pollen grains are lacking. Grafting of scions or twigs from special trees to trees of the same species is the most commonly used method of propagating southern pines. It is possible, but difficult, to root needle bundles and cuttings of twigs. Shortleaf pine can also be air-layered *(14)*.

Young shortleaf pines sprout vigorously at the root collar if the crown is killed or badly damaged, a feature which probably contributes much to the species' survival where other species decline. The ability to sprout profusely is generally confined to trees up to 15 to 20 cm (6 to 8 in) in diameter. Most sprouts eventually die, leaving from one to three stems to develop. Shoots also arise from buds developing in needle fascicles below the point of injury *(18)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Shortleaf pines (fig. 2) on good sites attain a height of 30 m (100 ft) or more and diameters (d.b.h.) of 61 to 91 cm (24 to 36 in). Heights of nearly 40 m (130 ft) and d.b.h. of 122 cm (48 in) have been recorded *(18)*, but the practice of growing trees to over 70 years of age is not commonly followed in managed stands because net growth rates decline rapidly. One of the biggest shortleaf pines grows in Mississippi. It measures 105 cm (41.5 in) in d.b.h. and 42 m (138 ft) tall and attests to the large size these trees may attain.

Considering the importance of shortleaf pine, the information available on growth and yield is limited *(40)*. The first variable-density yield information for a variety of sites and ages in natural stands was developed from forest survery data *(39,41)*. The model provides volume and basal area predictions for natural, even-aged, shortleaf pine stands in the West Gulf region. For example, a 60-year-old stand with a basal area of 16.1 m^2/ha (70 ft^2/acre) and a site index of 21.3 m (70 ft) would have a sawtimber volume of 119.8 m^3/ha (1,712 ft^3/acre) for trees 23 cm (9 in) d.b.h. and larger *(39)*. For trees 13 cm (5 in) d.b.h. and larger, the volume would be 129.6 m^3/ha (1,851 ft^3/acre)*(41)*. These yields are for a broad range of stand conditions, including unmanaged stands and those with a significant hardwood component. Managed stands should provide greater yields. Data from uneven-aged shortleaf pine stands in the Interior Highlands of Arkansas were used to construct a similar model *(42)*. After the cyclic harvest levels have stabilized, the periodic annual growth (based on International 1/4-inch rule) for these stands is 5.3 m^3/ha (381 fbm/acre), with a residual after cut volume of 89.3 m^3/ha (6,378 fbm/acre).

Stand structure and yield data for shortleaf pine plantations in the Tennessee, Alabama, and Georgia Highlands show that with a site index of 18.3 m (60 ft) at base age 25 years, mean annual increment of total volume culminates near age 20 *(54)*, at about 15.8 m^3/ha (225 ft^3/acre). Total volume yield (outside bark) of all trees at age 40, where the site index is 9.1 m (30 ft) and denisty is 3,090 stems per hectare (1,250/acre), is about 180 m^3/ha (2,570 ft^3/acre). For the same age and planting density, the volume where site index is 18.3 m (60 ft) is about 451 m³/ha (6,446 ft³/acre). Basal areas for these two stand conditions are 31 and 39 m²/ha (135 and 171 ft²/acre), respectively. The actual numbers of trees are 1,870 and 875/ha (757 and 354/acre). Thinnings in such stands will likely provide greater volume production through capture of mortality and will increase average diameter *(68)*.

Natural shortleaf pine stands in Missouri showed significantly higher net volume yields when thinned to about 21 m²/ha (90 ft²/acre) or above, at age 51. The presence of hardwoods reduced growth and yield of the stands by 8 to 12 percent *(48)*. In south Arkansas, annual growth of uneven-aged shortleaf-loblolly pine stands averaged 5.9 m³/ha (84 ft³/acre) during a 24-year measurement period *(44)*. Annual sawtimber growth of these stands averaged 6.0 m³/ha (432 fbm/acre).

Rooting Habit—Shortleaf pine seedlings can develop a taproot at an early age, which may become quite massive if allowed to grow uninhibited *(38)*. If the taproot is damaged, the seedling can grow a new one *(34)*. In much of the region where shortleaf pine grows, however, taproots do not develop because of shallow, rocky soils and in some cases hardpans. Lateral roots tend to grow near the soil surface; they are generally concentrated in the upper 46 cm (18 in) of the soil and rarely occur below a depth of 102 cm (40 in).

Tree growth response tends to be related to root development. The cross-sectional area of roots at groundline and the composite root area or sum of the areas of the first-order lateral roots plus the area of the taproot of 3- to 9-year-old shortleaf pines from Arkansas, Oklahoma, and Texas were found to be highly correlated. This suggests that basal stem diameter growth is directly related to root development *(11)*. Root systems of trees originating from natural or artificial seeding are more likely to have a single taproot than planted trees. Trees with root systems oriented downward have better height growth than trees with surface-oriented root systems *(26)*.

Reaction to Competition—Shortleaf pine is a shade-intolerant species and does not survive or grow well when suppressed *(16)*. Young shortleaf pines are generally slower growing and slower to dominate a site than loblolly pine or many hardwood competitors, but they usually will endure competition longer than its common associate, loblolly pine. Shortleaf pine can maintain dominance on most sites after it overtops competing vegetation, but in general hardwoods cannot be eliminated from pine sites *(7,9,10)*. On very good sites, however, it may not outgrow competing species such as sweetgum and red maple. Control of both woody and non-woody competition usually results in economic gains *(15,35)*.

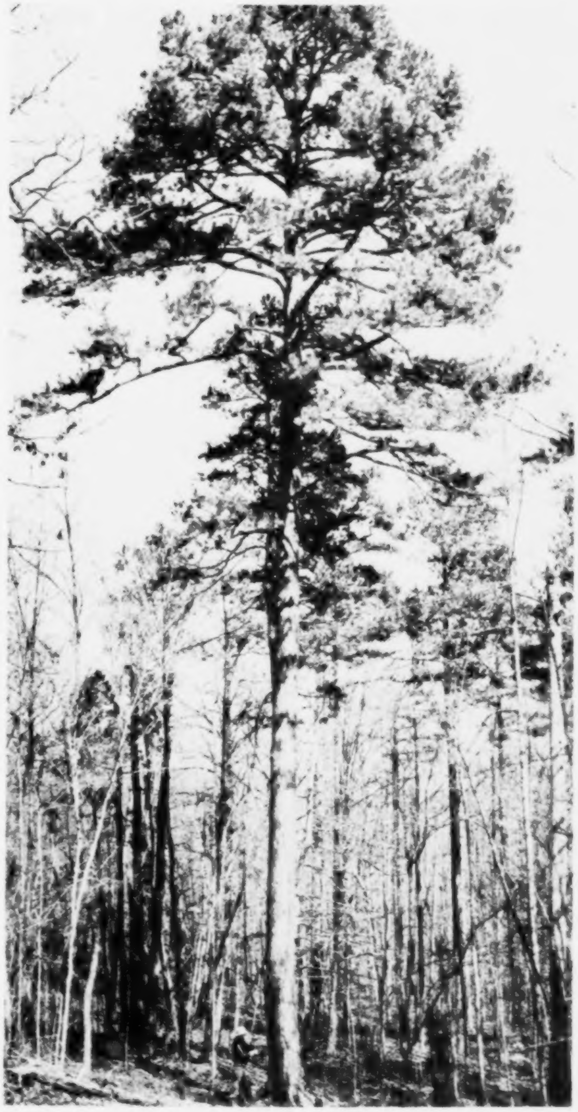

Figure 2—*A mature shortleaf pine.*

In young, well-stocked shortleaf pine stands, trees begin to compete with each other within a few years after establishment, and diameter growth rates decline *(69)*. Even though growth rates decline, shortleaf pine persists in very dense stands. Natural pruning occurs as the canopies close, but it is slower than on loblolly pine *(Pinus taeda)* or longleaf pine *(P. palustris)*. Shortleaf pine usually responds well to release, even when the trees are mature *(18,72)*. Removal of understory competition may also increase growth rates *(5)*.

Because of its intolerance to shade and other environmental factors, shortleaf pine commonly grows in even-aged stands (fig. 3) *(22,32)*. Natural and artificial regeneration methods are used to establish such stands *(4)*. Uneven-aged management is feasible, however, and may be an attractive alternative for small tracts of land *(44,45,67)*.

Damaging Agents—Littleleaf disease is the most serious pathlogical threat to shortleaf pine, occurring on poorly drained soils from Virginia to Mississippi and south to the Gulf Coast *(61)*. The disease results from combination of certain factors, including root destruction by *Phytophthora cinnamomi*, periodic excessive soil moisture deficits, poor aeration, low fertility, damage from nematodes, and perhaps toxic levels of manganese. These forces combine to impede mineral absorption, particularly nitrogen *(18,27)*. Symptoms of the disease usually appear when the stands are 30 to 50 years old, but seldom in stands less than 20 years old. Growth rates of infected trees may be greatly reduced, and mortality may be very high. Fertilization with nitrogen at 224 kg/ha (200 lb/acre) can relieve some of the symptoms in its early stages. No practical control measures for littleleaf disease in forest stands have been developed. It is suggested that proper site selection, species selection, and maintenance of stand vigor are the best defenses against this disease *(18,52)*.

Shortleaf saplings and older trees are moderately susceptible to attack by *Heterobasidion annosum*, a root rot. Losses in thinned plantations and occasionally in natural stands have occurred, but they have not been in general. Red heart, caused by *Phellinus pini*, may occur in older trees but is rare in stands under 80 years old. Several other relatively unimportant diseases occur in shortleaf pine *(27)*.

Shortleaf pine seedlings are subject to damping off and root rot caused by several fungi, usually when soils have a pH above 6 and weather conditions are wet. Foliage of shortleaf pine normally does not develop serious diseases, but at least eight needle rusts are known to attack the species *(27)*. Brown spot from *Scirrhia acicola* may be aggressive. The rust, *Cronartium comandrae*, has occasionally damaged shortleaf seedlings.

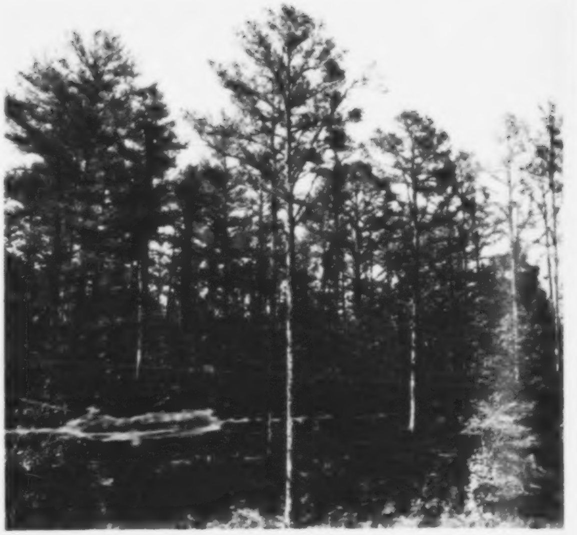

Figure 3—*Typical natural shortleaf pine stand showing abundance of understory hardwoods.*

Young shortleaf pines are attacked by Nantucket pine tip moth *(Rhyacionia frustrana)*. This insect has become a major pest in the eastern United States and may have greater impacts on growth than previously believed. Chemical control of this pest is difficult in forest situations, although early results of spray applications have shown promise. The red-headed pine sawfly *(Neodiprion lecontei)* is our most destructive sawfly, and shortleaf is one of its preferred species. Loblolly pine sawfly *(N. taedae linearis)*, attacks shortleaf pine in at least eight States. Reproduction weevils are the most serious insect pests of pine seedlings, reportedly killing 20 to 30 percent of seedlings planted in cutover pine lands. Pales weevil *(Hylobius pales)*, and pitch-eating weevil, *(Pachylobius picivorus)*, are most destructive species over the eastern and southern United States *(1,17)*.

The southern pine beetle *(Dendroctonus frontalis)* occasionally causes great losses. Other important insects are the pine engraver beetles *(Ips spp.)*, especially during severe droughts, and the black turpentine beetle *(Dendroctonus terebrans)*.

Shortleaf pine is generally fire resistant, but wildfires in young plantations are very damaging. The crowns are usually killed, but shortleaf pine will sprout from the base and form new stems. Larger trees may be killed by very hot fires, particularly if fuels near the tree bases are heavy. Fire damaged trees are also more susceptible to insect damage *(1*

Shortleaf pine is generally considered to be windfirm over most of its range, although trees may be uprooted by wind where root systems are shallow *(18)*. Shortleaf pines may also be damaged by severe ice storms. A single ice storm resulted in loss of almost one-third of the volume in a very heavily stocked shortleaf pine stand in north Arkansas *(37)*. Thinned, pole-size stands are especially susceptible to damage, which often includes main stem breakage.

Acid rain may reduce growth of shortleaf pine *(28)*. It may also result in aluminum toxicity to the roots of young trees, but could improve growth through increased availability of mineral nutrients *(49)*. Extreme drought can result in or contribute to mortality of shortleaf pine *(70)*.

Special Uses

Shortleaf pine is primarily used for lumber, plywood, other structural materials, and pulpwood. Even the taproots are used for pulpwood. The species was commonly planted on eroded lands in Mississippi *(68)* but does not produce as much litter as loblolly pine and therefore may be less desirable for some reclamation uses. Shortleaf pine is sometimes planted as an evergreen ornamental and as a screen in urban areas.

The seeds of shortleaf pine are eaten by birds and small mammals. Squirrels may cut the cones and eat the seeds before the cones open naturally *(23)*. The canopies of shortleaf pine provide protection from the wind and cold for many animals. Stands of shortleaf pine scattered through hardwood forests are especially beneficial to wildlife. Older shortleaf pines with red heart rot *(Phellinus pini)* are primary nesting trees for the red-cockaded woodpecker *(51)*.

Genetics

Because of shortleaf pine's wide distribution and the range in elevation at which it grows, considerable racial variation has developed. The Southwide Pine Seed Source Study indicated important racial differences in height, volume growth, survival, and degree of early cone production *(63,65)*. Seed collection and planting zones have been drawn for shortleaf pine on the basis of these results *(62,64)*. The zones are primarily a function of latitude, with much wider movement of seed being acceptable in an east–west direction than north–south. There is some indication that the shortleaf pine population west of the Mississippi River has an inherently faster growth rate than the eastern population *(64)*.

Other studies have revealed differences in height growth, volume growth, wood specific gravity, chemical content, and foliage color *(14)*. Shortleaf pine from some locations grew faster than loblolly pine, but loblolly was generally the faster growing species. In Georgia, South Carolina, and Virginia, shortleaf pine planted on sites where littleleaf disease was likely to occur revealed that trees were healthier from locations west to east, and those from upland locations were healthier than those from coastal plain areas. Specific gravity of shortleaf pine has been shown to increase slightly from the north to the south *(19)*, and monoterpene chemical composition of wood oleoresin as found to vary in a clinal pattern, with α-pinene increasing from east to west while ß-pinene decreased *(12)*.

Natural hybridization of shortleaf pine and loblolly pine west of the Mississippi River is considered to be extensive and is probably a cause of many inherent variations in the species *(24)*. Such hybridization would contribute to variation among trees through creation of intermediate types and introgression towards one or both parent species. The natural variations of shortleaf pine have been the basis for selecting trees having superior qualities. These qualities include growth rate, stem and crown form, resistance to littleleaf and other diseases, wood specific gravity, tracheid length, extractives, oleoresin content, and seed production *(14)*. Many of these traits have been the basis for selecting individual trees for seed orchards, which are rapidly becoming the primary source of seeds for planting programs. In 1974, there were 190.6 ha (471 acres) of shortleaf seed orchards in the United States, with 158.2 ha (391 acres) in Federal management *(56)*; more than half of the total acreage is in Arkansas.

Several artificial hybrids have been produced with shortleaf pine. They are of special interest because they offer the opportunity to combine specific qualities of individual species. For example, shortleaf pine can be crossed with slash pine *(Pinus elliottii)* to yield progeny that are resistant to fusiform rust, a disease to which slash pine is highly susceptible. Shortleaf pine has been successfully crossed with slash, loblolly, longleaf, and Sonderegger pines *(P. elliottii, P. taeda, P. palustris,* and *P. × sondereggeri) (50,55)*. Some of the hybrids have also been backcrossed. Shortleaf pine × loblolly pine hybrids have also shown resistance to fusiform rust, have grown as well as or better than one or both parents, and have shown increased resistance to cold and ice damage *(30)*. Characteristics of most shortleaf hybrids, as well as other pine hybrids, are intermediate between the parent species. Fusiform rust resistance of shortleaf × slash hybrids, however, is closer to shortleaf pine than slash pine *(66)*. The longleaf × shortleaf pine hybrid is difficult to produce and crosses have yielded only a few seedlings. These have shown intermediate characteristics, but seedling height growth was not delayed as it is characteristically for longleaf pine. Shortleaf × pitch pine *(P. echinata × P. rigida)* and Table Mountain × shortleaf pine *(P. pungens × P. echinata)* hybrids have also been produced and generally have intermediate characteristics *(14)*.

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Pinus edulis Engelm. Pinyon

Pinaceae Pine family

Frank P. Ronco, Jr.

Pinyon (*Pinus edulis*) is a small, drought-hardy, long-lived tree widespread in the southwestern United States. Its common name is derived from the Spanish *piñon* which refers to the large seed of *pino* (pine). For this reason the tree is known in the Southwest and throughout its range by this Spanish equivalent (*49*). Other common names are Colorado pinyon, nut pine, two-needle pinyon, and two-leaf pinyon (*50*). Its heavy, yellow wood is used primarily for fuel. Because of their delicate flavor its seeds are in much demand, making them its most valuable product.

Habitat

Native Range

As a codominant with juniper species (*Juniperus* spp.), pinyon trees (fig. 1) predominate in pinyon–

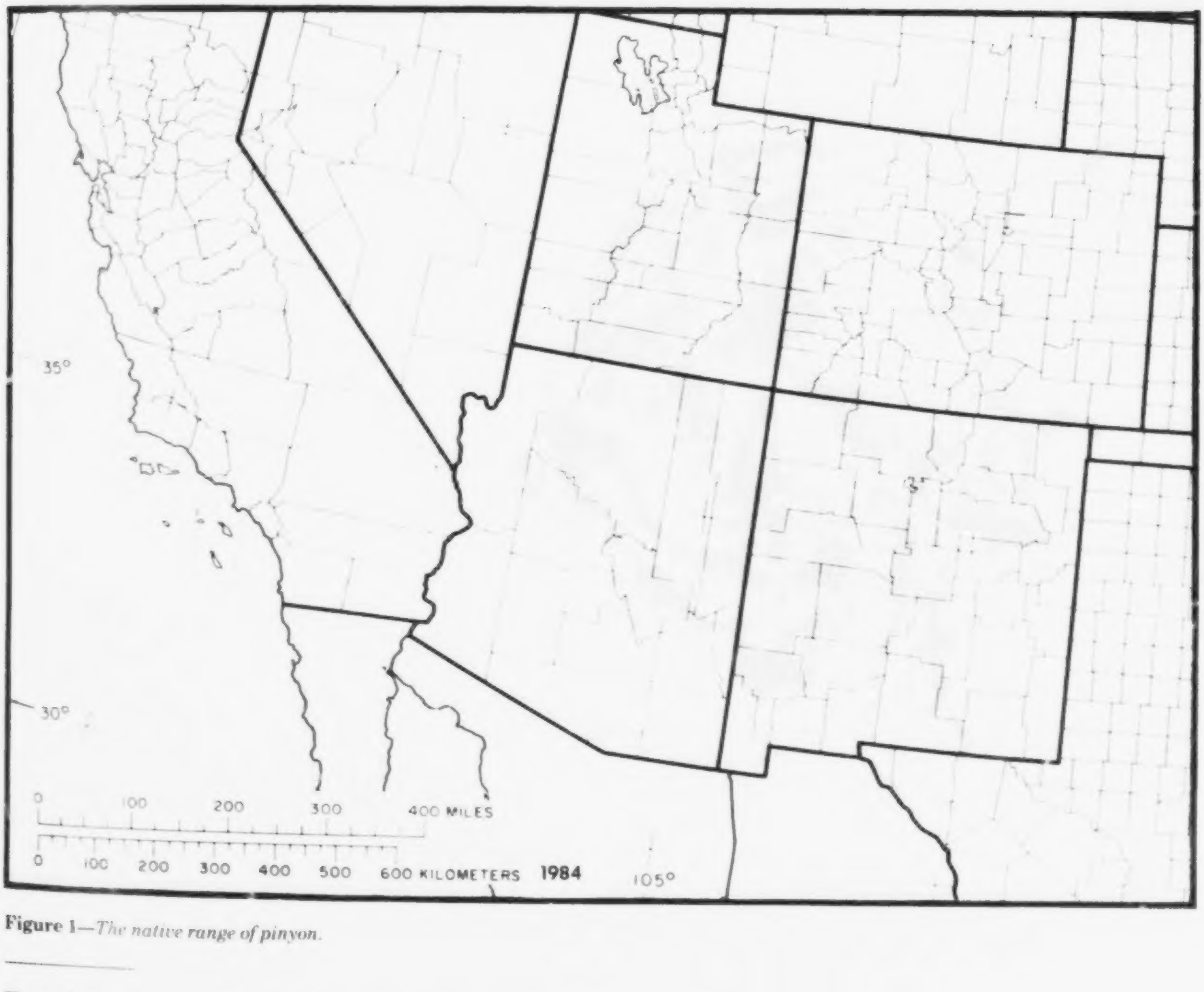

Figure 1—*The native range of pinyon.*

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juniper woodlands of the semidesert zone, which cover nearly 24.7 million ha (61 million acres), extending from Texas to California *(9)*. Woodlands in which pinyon is the major pine species cover about 14.9 million ha (36.9 million acres) in Arizona, Colorado, New Mexico, and Utah. Outliers in California, Oklahoma, Texas, and Wyoming contribute a relatively insignificant acreage to the total *(48)*. However, the outlier in California has been considered a population of 2-needled individuals of single-leaf pinyon *(Pinus monophylla)*, and more recently, a new species, California single-needle pinyon *(Pinus californiarum) (5,44)*.

Climate

The pinyon-juniper type occupies the lowest and warmest forested zone in the United States, with a climate generally characterized as semiarid, and locally as dry subhumid *(65)*. Summers are hot and winters relatively cold, especially in northern locations and at high elevations. A high percentage of clear days, intense solar radiation, and windy conditions favor high evapotranspiration rates *(67)*.

Annual precipitation, which varies widely throughout the type because of differences in elevation, topography, and geography, ranges from 250 mm (10 in) at low elevations where the type adjoins the desert or grassland vegetation to 560 mm (22 in) or higher at the upper reaches *(62,67,73)*. Locally, amounts as high as 690 mm (27 in) have been recorded, as along the Mogollon Rim in northern Arizona *(15)*.

Seasonal distribution, which also varies considerably, is related to prevailing storm patterns. In eastern New Mexico, for example, approximately 75 percent of the annual precipitation occurs during the warm season (April through September) from storms originating in the Gulf of Mexico, whereas the percentage decreases as these summer storms lose intensity during their northwesterly movement *(62)*. Nevertheless, summer precipitation throughout much of northern Arizona and the south-central and eastern portions of Utah is still about equal to, or slightly greater than, winter moisture *(14,42)*. Furthermore, as much as one-third of the rainfall may occur during July and August *(67)*. In contrast, woodlands of Nevada and northern Utah receive more precipitation during the cool season (October through March), primarily from Pacific winter and spring storms *(13,14)*. Snow depths are not great, except at higher elevations and more northerly latitudes, but even then, melt generally occurs within a few days, especially on south-facing slopes *(62)*.

The mean annual temperature in pinyon-juniper woodlands varies from 4° to 16° C (40° to 61° F); extremes may fall to -35° C (-31° F) and reach 44° C (112° F). January means may be as low as -10° C (14° F) in the more northerly portion of the type, and about 6° C (43° F) near the southern limits. Mean July temperatures are less variable, ranging from 20° to 27° C (68° to 81° F). The frost-free period ranges from about 90 to 205 days, the shorter period typifying more northerly latitudes and higher elevations *(59,67,73)*.

Because of wide variation in temperature and the amount and distribution of precipitation, the following classification has been proposed to better characterize the climate of pinyon-juniper woodlands in Arizona and New Mexico *(62)*:

	Precipitation	
Climate	**Winter**	**Summer**
	mm	
Cool, moist	230 to 280	180 to 230
Warm, moist	250 to 330	150 to 230
Cool, winter dry	130 to 180	180 to 230
Warm, winter dry	100 to 180	200 to 280
Cold, winter dry	100 to 150	200 to 250
Cold, summer dry	180 to 230	100 to 150
Warm, summer dry	180 to 230	100 to 150
	in	
Cool, moist	9 to 11	7 to 9
Warm, moist	10 to 13	6 to 9
Cool, winter dry	5 to 7	7 to 9
Warm, winter dry	4 to 7	8 to 11
Cold, winter dry	4 to 6	8 to 10
Cold, summer dry	7 to 9	4 to 6
Warm, summer dry	7 to 9	4 to 6

Soils and Topography

Pinyon-juniper woodlands are located mainly on the more rocky plateaus, mesas, foothill terraces, and lower mountain slopes; shrubs or grasses grow on finer soils in intervening valleys, canyons, or shallow washes. Such discontinuities have been attributed to fire history and soil-related differences. The oldest pinyons are frequently found on steep, rocky sites where fire occurrence and severity are probably lower than in intervening areas, and consequently less damaging to trees *(37,41,67,73)*.

Discontinuities ascribed to soil differences may in fact be related to the greater amounts of water that coarser soils make available to the tree, as the different soils are adjacent and there are no obvious differences in climatic factors. Furthermore, pinyon-juniper woodlands are found on a wide variety of soil depths and textures that range from coarse, rocky gravels to fine, compacted clays, indicating little if any correlation between these conditions and the presence of pinyon. Depth and texture, however, could affect productivity *(37,45,62,67)*.

Woodlands also are associated with a broad range of soil Great Groups, of which Haplustalfs of the order Alfisols, Ustochrepts of the order Inceptisols, and Ustorthents of the order Entisols are the most common *(37,52,76)*. Parent materials are equally varied. Sedimentary sandstones, limestones, and shales are most common, but materials of igneous origin, such as cinders and basalt, and those from metamorphic sources, also are found *(40,62,67)*. In some soils, carbonates may accumulate and form a petrocalcic horizon (hardpan) that may extend as deep as 1.5 m (5 ft), but is usually much shallower. Upper layers of woodland soils generally exhibit pH values ranging from about 7 to 8.4, but at higher and wetter elevations, soils tend to be slightly acid in reaction, approaching 6.5 *(31,37,43,45,69)*.

Pinyon-juniper woodlands are found between the low plains covered by grassland, desert shrub, or chaparral vegetation and the high mountains just below the zone dominated by either submontane shrubs or ponderosa pine *(Pinus ponderosa)*. The lower limit of growth is probably related more to the inability of pinyon trees—especially seedlings—to tolerate water stress arising from decreasing precipitation and subsequent reduction of total moisture, rather than to soil or temperature factors. In contrast, the upper limit appears to be a function of greater biotic competition resulting from increased moisture *(10,67)*.

In elevation, the woodlands lie mostly between 1370 and 2440 m (4,500 and 8,000 ft) *(67)*. Individual pinyons, however, may extend up to 3200 m (10,500 ft) on south- and west-facing slopes in the mixed conifer forests of Arizona *(70)*, while scattered juniper trees may descend to 910 m (3,000 ft) *(41)*. Although the range in any given locality is considerably narrower, the elevational band occupied by woodlands is a rather uniform span of about 610 m (2,000 ft). There is a tendency, however, for the entire band to decrease in elevation in a southeasterly direction *(72)*. In Arizona, the majority of the type is found between 1370 and 1980 m (4,500 and 6,500 ft), whereas in Colorado, the band extends from 1830 to 2440 m (6,000 to 8,000 ft). The bulk of the woodland in New Mexico and Utah occupies a zone from 1520 to 2130 m (5,000 to 7,000 ft).

Associated Forest Cover

Pinyon is a minor component of the following forest cover types *(61)*: Bristlecone Pine (Society of American Foresters (Type 209), Interior Douglas-Fir (Type 210), Rocky Mountain Juniper (Type 220), Interior Ponderosa Pine (Type 237), Arizona Cypress (Type 240), and Western Live Oak (Type 241). It is an integral component in Pinyon-Juniper (Type 239) over a large area. However, as the type extends westward, pinyon is replaced by singleleaf pinyon *(Pinus monophylla)* in Nevada and some localities in western Utah and northwestern Arizona *(4,67)*. Southward along the Mexican border, Mexican pinyon *(P. cembroides* var. *bicolor)*, recently given separate species status as border pinyon *(P. discolor)*, becomes the dominant tree in the woodlands *(6,48,49)*.

Common associates of pinyon over most of its range are oneseed juniper *(Juniperus monosperma)* and Utah juniper *(J. osteosperma)*; redberry juniper *(J. erythrocarpa)*, also a one-seeded juniper, is confined to the southern portion. Alligator juniper *(J. deppeana)* and Rocky Mountain juniper *(J. scopulorum)* are also found in some localities *(1,4,67)*. Oneseed juniper predominates in east-central Arizona and most of New Mexico, and extends into western Texas and southcentral Colorado. Rocky Mountain juniper is also a common component in northern New Mexico and the western half of Colorado, but it is found over most of the woodlands as well. It usually grows at higher elevations and is seldom dominant in the stand. Utah juniper is the codominant associate in Utah, northern Arizona, western Colorado, and northwestern New Mexico. At higher, more mesic elevations in southern and western New Mexico and westward into central Arizona, alligator juniper commonly forms a component of stands.

Although pinyon-juniper woodlands consist of relatively few tree species, stands exhibit considerable diversity in appearance and composition *(4)*. Some have nearly closed canopies of a single tree species with little or no understory vegetation.

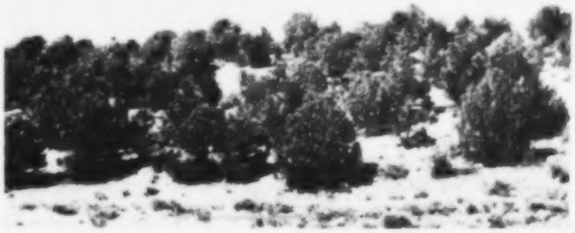

Figure 2—*The bushy form of trees in pinyon-juniper woodlands suggests an evergreen forest in which development has been stunted.*

Others are open, with widely scattered pines, junipers, or both among grasses and shrubs. A typical pinyon–juniper woodland, with its many-branched trees resembling shrubs, has the appearance of a stunted coniferous forest (fig. 2).

Any particular stand usually contains only a few different plant species, but because of the wide distribution of the type, the total flora associated with woodlands is quite varied *(4,67,73)*. Common tree and shrub associates include: Gambel oak *(Quercus gambelii)*, gray oak *(Q. grisea)*, shrub live oak *(Q. turbinella)*, true mountain-mahogany *(Cercocarpus montanus)*, curlleaf mountain-mahogany *(C. ledifolius)*, antelope bitterbrush *(Purshia tridentata)*, big sagebrush *(Artemisia tridentata)*, black sagebrush *(A. nova)*, serviceberry *(Amelanchier* spp.), rabbitbrush *(Chrysothamnus* spp.), Mexican cliffrose *(Cowania mexicana)*, Apache-plume *(Fallugia paradoxa)*, skunkbush *(Rhus trilobata)*, Mormon-tea *(Ephedra* spp.), yucca *(Yucca* spp.), opuntia *(Opuntia* spp.), broom snakeweed *(Gutierrezia sarothrae)*, and buckwheat *(Eriogonum* spp.).

Some of the more important herbaceous plants are goosefoot *(Chenopodium graveolens)*, rock goldenrod *(Solidago pumila)*, gilia *(Gilia* spp.), penstemon *(Penstemon* spp.), segolily *(Calochortus nuttallii)*, globemallow *(Sphaeralcea* spp.), white aster *(Aster hirtifolius)*, hymenopappus *(Hymenopappus filifolius* var. *lugens)*, Indian ricegrass *(Oryzopsis hymenoides)*, dropseed *(Sporobolus* spp.), needleandthread *(Stipa comata)*, squirreltail *(Sitanion hystrix)*, Junegrass *(Koeleria pyramidata)*, galleta *(Hilaria jamesii)*, blue grama *(Bouteloua gracilis)*, sideoats grama *(B. curtipendula)*, ring muhly *(Muhlenbergia torreyi)*, western wheatgrass *(Agropyron smithii)*, bluebunch wheatgrass *(A. spicatum)*, slender wheatgrass *(A. trachycaulum)*, downy chess *(Bromus tectorum)*, and threeawn *(Arisitada* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pinyon is considered monoecious, the male and female strobili being borne on the same tree *(67)*. However, dioecy has been observed under certain environmental conditions associated with moisture stress and insect damage *(23,74)*. Although ovulate cones require most of three growing seasons to mature, the stages of growth vary with elevation, weather, and individual trees. In general, winter buds containing the strobili primordia begin to form in August, and by October of the first year are fully formed. Bud growth the following year is resumed near the first of May for staminate cones, and about mid-May for ovulate cones. By mid-June, staminate cones are mature, and ovulate cones become visible and receptive to pollen. Pollination is completed by the end of June when cone scales close, and a period of rapid growth of cones and seed commences, terminating at the end of August. During the third year, conelets start growth about the first of May, and fertilization occurs in early July. Shortly thereafter, cones and seeds reach full size, and seed coats darken and harden. Seeds mature early in September, and cone opening begins during mid-month and extends for about a 50-day period.

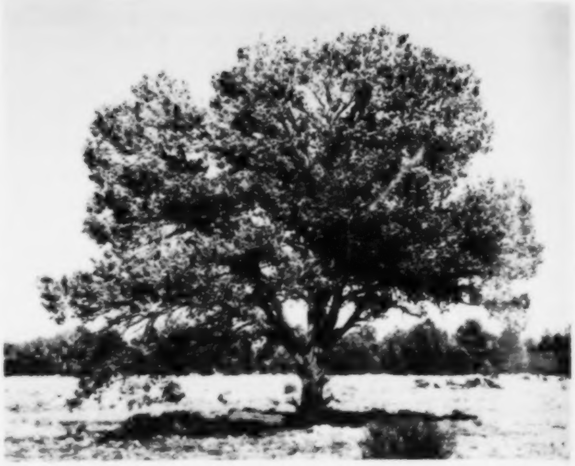

Figure 3—*A mature, broad-crowned pinyon such as this should b a heavy seed producer.*

Seed Production and Dissemination—Trees reach cone-bearing age when relatively young: 25 years old and 1.5 to 3.0 m (5 to 10 ft) tall. Seeds are not produced in quantity, however, until age 75 to 100, but the long-lived pinyons continue to bear for a few centuries. A mature pinyon usually has a broad and rounded or irregular crown, which is often almost as wide as the tree height. Such trees are the heaviest seed producers, since cones are found mostly in the upper half of the crown near the ends of branches (fig. 3). Each cone contains about 10 to 20 seeds, which average only 4,190/kg (1,900/lb) because of their large size. A large tree in a good crop year may yield over 9.1 kg (20 lb) of seed, and better stands will produce an estimated 336 kg/ha (300 lb/acre). Germinative capacity of seeds may range between 83 and 96 percent; germinative energy is about 80 percent in 7 days *(9,30,67,68)*.

Cone crops are either good or poor, often with cones practically absent, but seldom intermediate

(67). Although good crops tend to be localized and occur at irregular and infrequent intervals, some are found nearly every year somewhere over the widespread range of the species. Furthermore, cone bearing tends to be synchronous over large geographical areas, a condition considered to be an evolved mechanism to counteract seed predation *(46)*. On an average, substantial crops are produced every 4 to 7 years, but shorter intervals of 2 to 5 years elapse with individual trees or in certain localities *(9)*. Generally, crops occur more frequently on better sites over the optimum range of pinyon than at the extreme limits.

The large, wingless seeds of pinyon are not adapted to wind dissemination. Instead, seed dispersal beyond tree crowns depends upon the behavior of four corvid species of birds—Clark's nutcracker, Steller's jay, scrub jay, and pinyon jay *(8)*. Although these species eat great quantities of seed during the fall and may be greater predators than rodents, they also cache large amounts for consumption during ensuing winter months. Some of these buried seeds are not recovered by the birds, thus providing a seed source for subsequent germination and seedling establishment, particularly if caches are located in a suitable microenvironment, such as alongside shrubs or downed trees *(46)*. Steller's and scrub jays collect seed only from open cones. In contrast, pinyon jays and Clark's nutcrackers forage from green cones, from which seeds are deftly extracted, and then from open cones as the season progresses *(8,71)*.

Clark's nutcrackers and Steller's jays probably contribute little towards regenerating existing woodland sites because their caches are located at higher elevations in ponderosa pine and mixed conifer forests or in the ecotone above pinyon–juniper woodlands *(8)*. Thus, these species tend to expand woodlands to upper elevations. In contrast, scrub jays and pinyon jays cache seeds in woodland areas, the former in small, local territories, whereas the latter transport seeds up to 12 kilometers (7.5 mi).

Pinyon jays live in flocks of 50 to 500 birds, and it has been estimated that during a substantial seed year in New Mexico, about 4.5 million seeds were cached by a single flock *(46)*. Even scrub jays, which do not exhibit flock behavior can be important seed dispersers—a single pair of birds may harvest and cache about 13,000 seeds from a particular crop. Pinyon jays can carry an average of up to 56 seeds in an expandable esophagus. Scrub jays lack this adaption, and the amount of seed that can be transported at one time is limited to 5 or fewer seeds held in the mouth and bill. The majority of caches by pinyon and scrub jays are single-seeded, and are located in the transition zone between mineral soil and the overlying organic material *(8,71)*.

Although rodents are known to cache seed, they should not be considered effective seed dispersers because caches are located in middens or underground chambers where conditions are not suitable for germination or seedling establishment. Instead, rodents, such as cliff chipmunks, pinyon mice, and woodrats, are major predators, caching as much as 35 to 70 liters (1 to 2 bu) of good seed *(46,67)*. Furthermore, limited data indicate that rodents consume large quantities of seeds taken from bird caches *(32)*.

It has been suggested that pinyon trees and seed eating birds have evolved coadaptive traits that enhance survival of both organisms. The seed dispersing and caching behavior of birds appears related to certain traits of the trees: large, thin-coated seeds with high energy values, different colored seedcoats that aid visually oriented seed harvesters to distinguish edible from aborted seeds, upward orientation of cone and scale angle for increased seed visibility, and prolonged seed retention in open cones because of cone orientation and deep depressions and small flanges on cone scales *(70)*. Furthermore, the mutual dependence of birds and trees appears more complex than just their respective roles of seed dispersing and food providing agents. Gonadal activity of pinyon jays, for example, is increased before the breeding season by the combined effect of photoperiod, the appearance of cones, and a diet of seeds *(46)*.

Seedling Development—Natural regeneration is difficult to achieve, primarily because of unfavorable climatic conditions, but seed predation and heavy grazing pressure, especially by sheep and goats, also play a role *(67)*. Although pinyon grows best in full sunlight and can germinate in the open, seedlings must be protected from the harsh environment *(21,31,35,46,49)*. Regeneration is usually achieved in the shade of tree canopies, under shrubs such as rabbitbrush, mountain-mahogany, and sagebrush, or alongside fallen trees.

Optimum germination temperature for pinyon seed is about 21° C (70° F). Germination is epigeal *(68)*. Preliminary studies indicate that germination can be significantly improved by washing seeds for 48 hours in running tap water. Cold stratification for 30 or 60 days increases speed of germination but not the percentage. Treatment with hydrogen peroxide to suppress mold and enhance germination generally is not effective. Seeds germinate in spring and summer following dispersal, depending on soil moisture and temperature, with summer germination coinciding with the onset of the rainy season. Also, seedling establishment probably depends on an adequate moisture supply during the first summer *(29,30,54,66,68)*. Growth throughout the seedling stage is extremely slow, often with only primary needles developing the first year, and subsequent height growth averaging 2.5 to 5.0 cm (1 to 2 in) per year *(67)*.

Vegetative Reproduction—Pinyon is not known to reproduce vegetatively.

Sapling and Pole Stages to Maturity

Growth and Yield—Pinyon grows best on the higher, wetter sites of the woodland zone, just below the ponderosa pine type *(40,67)*. At these elevations trees reach their tallest heights and tend to develop single stems (fig. 4). At lower elevations, in contrast, bushy and sprawling crowns are characteristic. Pinyons may be multistemmed, although to a lesser extent than junipers. They usually exhibit straight, but short and rapidly tapering boles, which diverge into many large sinuous branches.

Growth of pinyon, though maintained with little loss of vigor throughout the life of the tree, is extremely slow. Height growth of saplings, for example, is only about 10 to 15 cm (4 to 6 in) yearly, and mature trees grow even more slowly, averaging 5 to 10 cm (2 to 4 in) per year. Diameter growth also is slow, especially on poor sites, where 80 to 100 years can elapse before diameters at breast height reach even 10 to 15 cm (4 to 6 in). On better soils, however, 150-year-old trees may grow to a diameter of 30 cm (12 in). Mean annual diameter growth of pinyon culminates at about 1.8 cm (0.7 in) per decade, when trees are approximately 50 years old. The gross annual increment on sample plots in northern New Mexico woodlands also reflects the slow growth rate, averaging about 0.42 m^3/ha (6 ft^3/acre) for pinyon alone, and 0.66 m^3/ha (9.5 ft^3/acre) for all species. Gross cordwood increment for all species was 0.88 m^3/ha (0.14 cord/acre) *(38,66,67)*.

Pinyon is a long-lived tree, maturing in 75 to 200 years. Dominant trees in a stand are often 400 years old, and pinyons 800 to 1,000 years old have been found. Depending on the site, mature trees range between 3.0 and 15.5 m (10 to 51 ft) in height and 15 to over 76 cm (6 to 30 in) in d.b.h. Although large trees are common, especially in northern New Mexico, pinyons generally are small trees, usually less than 10.7 m (35 ft) tall and 46 cm (18 in) in diameter *(66,67)*. The largest living pinyon recorded grows in New Mexico and measures 172 cm (68 in) in d.b.h., 21.0 m (69 ft) in height, and has a crown spread of 15.8 m (52 ft) *(2)*.

Because of the growth habit of woodland species, tree volumes are not only difficult to measure but can vary more than 300 percent for trees of the same diameter. There is less variation in well-formed trees, however, and the gross volume of a representative pinyon with a basal diameter of 30 cm (12 in) and 7.6 m (25 ft) tall is 0.22 m^3 (7.7 ft^3), measured to a 10-cm (4-in) top. Woodland volumes vary considerably, depending on species composition and density. In northern New Mexico and Arizona, mixed stands may contain cordwood volumes ranging from about 5.0 to 157.4 m^3/ha (0.8 to 25 cords/acre), with average volumes of about 69.3 m^3/ha (11 cords/acre). Cordwood volumes of nearly pure pinyon stands average about 75.6 m^3/ha (12 cords/acre). Low volumes are a reflection of the small trees generally associated with woodlands. The average size tree in

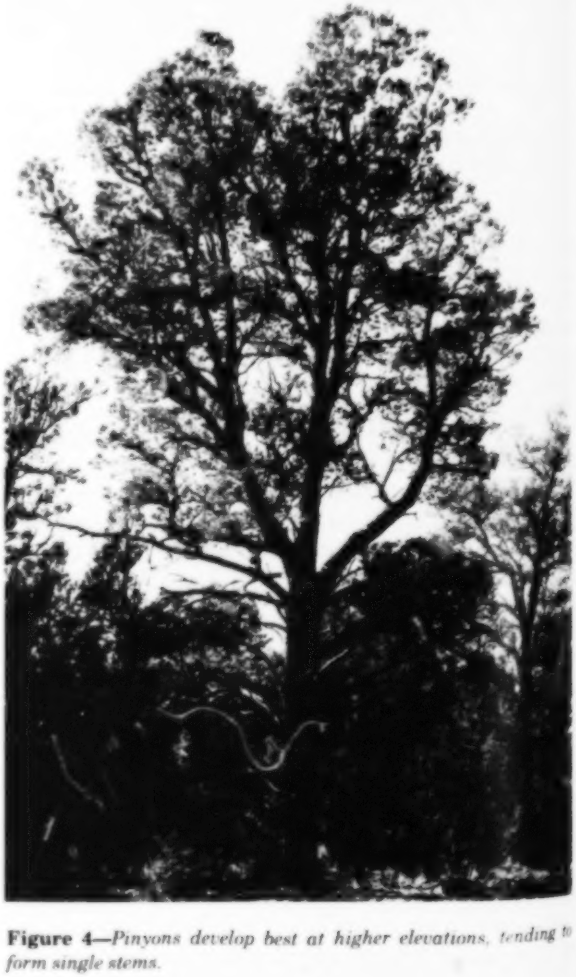

Figure 4—*Pinyons develop best at higher elevations, tending to form single stems.*

many New Mexico stands is only 15 cm (6 in) in diameter at ground line and about 2.7 m (9 ft) tall *(16,67)*.

The density of pinyon in woodlands varies considerably, ranging from few or none to several hundred stems per hectare. Nevertheless, the density in a typical northeastern Arizona stand averages about 235/ha (95/acre) in stems less than 7.6 cm (3 in) in d.b.h.; 200/ha (81/acre) from 7.6 to 15 cm (3 to 6 in) in d.b.h.; and 89/ha (36/acre) more than 15 cm (6 in) in d.b.h. *(67)*. Mixed woodlands are denser and more productive than pure stands of either pinyon or juniper, and can approach or exceed 3,459 stems/ha (1,400/acre) *(9,57)*. The higher values have been attributed to differences in rooting habit and drought tolerance of the two species. The shallower penetrating roots of pinyons limit interspecific root competition for soil moisture in mixed stands. This, combined with the lower photosynthetic rate of pinyons compared to that of junipers at higher water stresses, allows more complete site utilization in mixed stands *(10,25,57)*. The average number of pinyons suitable for Christmas trees varies from a few trees per acre to a fairly large number.

Rooting Habit—The rooting habit of pinyon is characterized by both lateral and vertical root systems *(67)*, but roots of pinyons less than 3 m (10 ft) tall have been traced to depths 6.4 m (21 ft) in underlying rock *(25)*. Taproots and some laterals that penetrate downward, however, grow horizontally when they encounter an impenetrable horizon or bedrock. Laterals develop at a depth of about 15 to 41 cm (6 to 16 in) and can exceed the crown radius by a factor of two or more. Taproot growth of seedlings is rapid, averaging 17 to 27 cm (7 to 11 in) in length for 1-year-old seedlings *(35)*. The extensive root system and relatively rapid rate of root elongation, especially of young seedlings, enhance the ability of pinyon to survive under arid environments.

Reaction to Competition—Pinyon is a sun-adapted plant and is classed as intolerant of shade *(67)*. It also appears unable to compete with grasses for moisture during the seedling stage following germination *(4)*.

Secondary succession following fire or other severe disturbance in pinyon–juniper woodlands appears to follow the general successional model shown in figure 5 *(3)*. However, the first herbaceous species to become established after a fire are often those that were present in the stand before disturbance *(19)*. The shrub stage, often consisting of sagebrush, a common associate in the woodlands, becomes prominent after about 12 years *(11)*. Junipers, which appear to have a wider ecological amplitude than pinyons because of their greater drought resistance, are usually the first trees to regenerate *(10,12,75)*. They rapidly increase in density after 45 years, and dominate the site at 70 years. Thereafter, pinyons tend to succeed junipers at rates determined by available seed sources until the shrub understory is essentially eliminated. If disturbances are less severe, as when cabling, chaining, or bulldozing is used to remove tree cover for range improvement, many small surviving pinyons and junipers and newly established seedlings, reforest the site in about 2 to 3 decades *(55,56,64)*. Under some conditions, however, natural regeneration can take much longer *(60)*.

Considerable evidence has accumulated to show that the woodlands, especially those dominated by singleleaf pinyon, are invading areas below their historic elevational limits *(3,12,17,41)*. Furthermore, tree density appears to be increasing in some stands that existed before the invasion period. Pinyon–juniper woodland expansion since the time of settlement has been attributed to several factors, including possible climatic changes, control of fire, increased populations of seed-dispersing birds and mammals, and reduced competition from grasses resulting from overgrazing by livestock or the allelopathic influence of juniper foliage and litter *(20,39)*.

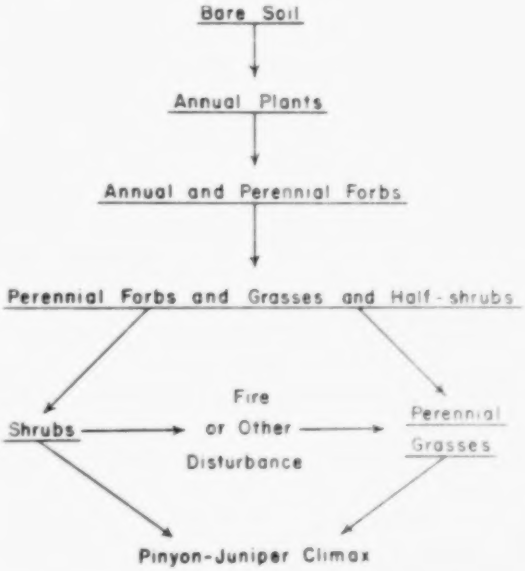
Bare Soil
Annual Plants
Annual and Perennial Forbs
Perennial Forbs and Grasses and Half-shrubs
Shrubs
Fire or Other Disturbance
Perennial Grasses
Pinyon-Juniper Climax

Figure 5—*Possible seres and pathways of secondary succession following disturbance in pinyon-juniper woodlands (3).*

Damaging Agents—Small pinyons 1 to 2 m (3 to 6 ft) tall are readily killed by fire, but larger trees appear more resistant. Fire is generally not a serious problem, however, because stands are open and understory fuels are sparse. Where vegetation is dense and weather conditions favorable, fire has been effective as a treatment for converting woodlands to grasslands *(3,18,40)*.

Among insects most commonly attacking the vegetative portion of trees are pinyon pitch nodule moth *(Petrova albicapitana arizonensis)*, tiger moth *(Halisidota ingens)*, mountain pine beetle *(Dendroctonus ponderosae)*, pinyon sawfly *(Neodiprion edulicolus)*, adelgid *(Pineus coloradensis)*, pinyon needle scale *(Matsucoccus acalyptus)*, pine needle scale *(Chionaspis pinifoliae)*, Arizona fivespined ips *(Ips lecontei)*, pinyon ips *(Ips confusus)*, pinyon needle miner *(Coleotechnites edulicola)*, pinyon tip moth *(Dioryctria albovittella)*, and gallmidges *(Pinyonia* spp., *Janetiella* spp., and *Contarinia* spp.) *(22,24,27,28,63,67)*. The most damaging cone and seed insects include cone moths *(Eucosma bobana)* and the pinyon cone beetle *(Conophthorus edulis)*. Many species of nematodes, especially in the *Helocotylenchus*, *Tylenchus*, and *Xiphinema* genera, are parasitic on pinyon roots, but their effect on growth in natural stands is unknown *(53)*.

A number of foliage diseases have been reported on pinyon, including needle casts *(Elytroderma deformans* and *Bifusella saccata)* and needle rusts *(Coleosporium jonesii* and *C. crowellii) (36,67)*. Pinyon blister rust *(Cronartium occidentale)* and pinyon dwarf mistletoe *(Arceuthobium divaricatum)* cause stem diseases, the latter being considered the major pathogen of pinyon. *Verticicladiella wagenerii*, a root rot, is also ranked high as a damaging agent; principal heart rots are red-ring rot *(Phellinus pini)* and brown cubical rot *(Fomitopsis pinicola)*. *Armillaria mellea* and *Phaeolus schweinitzii* are not particularly important diseases, but both cause root rot and butt rot.

Special Uses

Firewood is the product derived from pinyon-juniper woodlands that has been used most widely and for the longest time and it continues to be the primary energy source for the rural population of small communities in much of the Southwest *(9,60)*. Pinyon is preferred for fuelwood since it has a higher heat value than any of its associates except the oaks and burns with a pleasing and distinctive aroma.

Although pinyon has physical properties similar to those of ponderosa pine and is suitable for processing, it is not extensively used for sawn products because of poor growth form and small size *(9,51)*. Specialized woodworking shops use pinyon for novelties, and small sawmills produce mine timbers and railroad ties. The ties are used primarily in open pit mines because of their toughness and resistance to breakage during frequent rail line shifts. Pinyon has been used for pulping in the Southwest, but only to alleviate shortages of normally used mill-residue chips and pulpwood of other species. It is also occasionally processed for charcoal.

The edible nuts of pinyon are probably the most valuable product of the species and are in great demand because of their delicate flavor *(9,67)*. Annual nut crops have been estimated to average between 454 000 and 907 000 kg (1 to 2 million lb), reaching 3.6 million kg (8 million lb) in an exceptionally productive year. Commercial crops are practically nonexistant in some years, however. Nuts are commonly sold and consumed after roasting in the shell, but small quantities are sold raw. A limited retail market exists for shelled nuts, which have also been used in candies and other confections.

Pinyons have been cut for private use for Christmas trees for many years and have recently appeared on commercial lots *(9)*. In states with large acreages of pinyon-juniper woodlands, up to 40 percent of the yearly harvest in the past has been reported as pinyon. Demand has decreased since 1960, however, when 294,000 trees were harvested, ranking pinyon as 13th nationally. The decline has been attributed to an increasing supply of other plantation-grown species and the scarcity of high-quality trees in easily accessible stands.

Pinyon-juniper woodlands over the past 400 years have been, and will continue to be, grazed extensively *(62)*. Futhermore, range improvement practices to increase forage for wildlife and livestock have removed the woodland trees over large areas. Woodland watersheds also have been mechanically cleared or chemically treated in the past, but future treatments may be limited to specific areas, because the possibility of generally increasing water yield does not appear promising *(7,9,15)*.

Pinyon-juniper woodlands provide a habitat for a varied wildlife population *(26)*. Mule deer, white-tailed deer, elk, desert cottontail, mountain cottontail, and wild turkey provide increasing hunter recreation. Pinyon nuts are a preferred food for turkeys, but in poor seed years, juniper mast is extensively consumed *(58)*. Similarly, deer subsist on browse species, but pinyon is a common food particularly during harsh winters with deep snows *(33,34)*.

Genetics

Population Differences

A form of pinyon that extends southeastward from northwestern Arizona into southwestern New Mexico in the mountains south of the Mogollon Rim has been classified as a taxonomic variety, *P. edulis* var. *fallax* *(47)*. Others considered it a local variant of singleleaf pinyon *(44)*. More recently, however, it has been recognized as a subspecies of a newly described species of nut pine—*Pinus californiarum* subsp. *fallax* (Arizona single-needle pinyon) *(5)*.

Practically no information is available regarding population differences of pinyon. Considering the wide range of the species and the different environmental conditions under which it grows, differences would be expected. It has been reported that seed size is relatively consistent from year to year in individual trees but varies among trees *(67)*. Also, some trees generally produce more cones than others, and some bear larger cones with more seeds per cone.

Races and Hybrids

No races of pinyon have been recorded. Natural hybridization has been reported between pinyon and singleleaf pinyon in three zones common to the species—the eastern edge of the Great Basin, the mountains south of the Colorado Plateau, and areas adjacent to the Colorado River and its major drainages *(44)*. The two species also have been artificially crossed. Pinyon and the newly described Arizona single-needle pinyon also are known to hybridize *(5)*.

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Pinus elliottii Engelm. Slash Pine

Pinaceae Pine Family

Richard E. Lohrey and Susan V. Kossuth

Slash pine *(Pinus elliottii)* is one of the hard yellow pines indigenous to southeastern United States. Other names occasionally used for this species include southern pine, yellow slash pine, swamp pine, pitch pine, and Cuban pine. It is one of the two southern pines used for naval stores and one of the most frequently planted timber species in North America. Two varieties are recognized: *P. elliottii* var. *elliottii*, the slash pine most frequently encountered, and *P. elliottii* var. *densa*, that grows naturally only in the southern half of peninsula Florida and in the Keys.

Habitat

Native Range

Slash pine (fig. 1) has the smallest native range of the four major southern pines. The range extends over 8° latitude and 10° longitude, and 45 percent of the present growing stock is in Georgia *(53)*. Slash pine grows naturally from Georgetown County, SC, south to central Florida, and west to Tangipahoa Parish, LA. Its native range includes the lower Coastal Plain, part of the middle Coastal Plain, and the hills of south Georgia. The species has been established by planting as far north as Tennessee, in north central Georgia, and Alabama. It has also been planted and direct-seeded in Louisiana and eastern Texas where it now reproduces naturally.

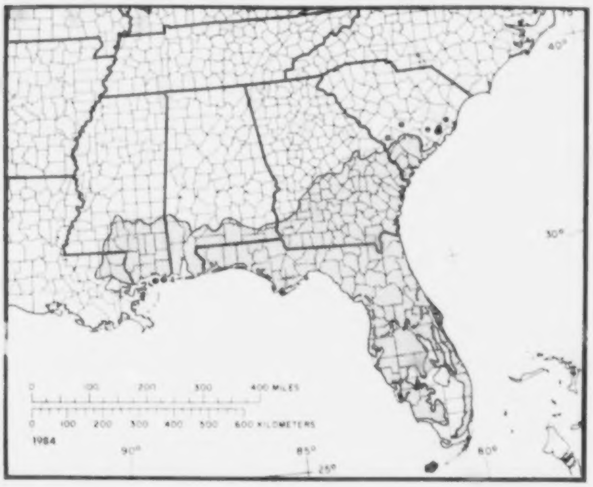

Figure 1—*The native range of slash pine. The broken line separates northward the typical variety and southward, South Florida slash pine,* P. elliottii *var.* densa.

Within its natural range, the distribution of slash pine was initially determined by its susceptibility to fire injury during the seedling stage. Slash pine grew throughout the flatwoods of north Florida and south Georgia.

It was also common along streams and the edges of swamps and bays *(21)*. Within these areas either ample soil moisture or standing water protected young seedlings from frequent wildfires in young forests.

With improved fire protection and heavy cutting of longleaf pine *(Pinus palustris)*, slash pine has spread to drier sites, replaced longleaf pine in mixed stands, and invaded abandoned fields. This increase in acreage was possible because of slash pine's frequent and abundant seed production, rapid early growth, and ability to withstand wildfires and rooting by hogs after the sapling stage.

Climate

The climate within the natural range of slash pine is warm and humid with wet summers and drier falls and springs. Rainfall averages about 1270 mm (50 in) per year and summer rains of 13 mm (0.5 in) or more occur about four times per month. The mean annual temperature in the slash pine region is 17° C (63° F), with extremes of 41° C (106° F) and -18° C (0° F), and a growing season of 250 days. It has been suggested that the average minimum temperature may be the most critical factor limiting the distribution of slash pine; however, precipitation, fire, or competition may be important in specific areas *(21)*.

Soils and Topography

Soils within the range of slash pine are mostly Spodosols, Ultisols, and Entisols. Spodosols and Entisols are common along the coasts of Florida while the Ultisols are in the northern part of the range. The most frequently found suborders are Udults, Aquults, Psamments, and Aquods. Topography varies little throughout the southeastern Coastal Plain, but

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small changes in elevation frequently coincide with abrupt changes in soil and site conditions.

Although slash pine is adaptable to a variety of site and topographic conditions, it grows best on pond margins and in drainages where soil moisture is ample but not excessive and the soil is well aerated. Growth is unsatisfactory on deep, well drained sands (sandhills) and on poorly drained savanna soils with high water tables (crawfish flats). Growth is intermediate on inadequately drained soils. Specific factors related to height growth, and hence to productivity, vary somewhat, but the most influential are those related to the amount of water or space available to tree roots.

Height growth of slash pine plantations in Florida was estimated from three soil factors: depth to a fine textured horizon, depth to a mottled horizon, and silt plus clay content of the finest textured horizon in the soil profile. The first two alone explained 89 percent of the variation in height at a given age and gave height estimates adequate for field use *(21)*. Where internal drainage was adequate, the height of slash pine increased directly with the amount of silt and clay in the subsoil *(12)*. Average site index (base age 50 years) ranged from 22.9 m (75 ft) for sands and loamy sands to 27.4 m (90 ft) for silty clays and other fine textured soils.

In the Carolina sandhills, slash pine heights increased with thickness of the A_1 soil horizon and decreased with depth to fine textured horizons *(44)*. In southeastern Louisiana, site index increased with depth of the least permeable layer, sand content of the subsoil, and degree of internal drainage. Site index decreased where the least permeable layer was too deep, the topsoil was too sandy, or the soil was excessively drained internally *(36)*.

Mean total height of dominants and codominants was related to seasonal rainfall, slope, and potential available moisture storage of the subsoil in 87 test plantings throughout Louisiana and southern Mississippi. Optimum conditions within the range of data were 610 mm (24 in) of rain from April through September, 790 mm (31 in) of rain from October through March, 5 percent slope, and 7 percent available moisture storage capacity in the subsoil. Dominant and codominant trees average 19.6 m (64.3 ft) tall at 20 years under these conditions *(49)*.

Associated Forest Cover

Slash pine is a major component of three forest cover types including Longleaf Pine–Slash Pine (Society of American Foresters Type 83), Slash Pine (Type 84), and Slash Pine–Hardwood (Type 85) *(18)*. The species is also included as an associate in the following cover types:

70	Longleaf Pine
74	Cabbage Palmetto
81	Loblolly Pine
82	Loblolly Pine–Hardwood
97	Atlantic White-Cedar
98	Pond Pine
100	Pondcypress
103	Water Tupelo–Swamp Tupelo
104	Sweetbay–Swamp Tupelo–Redbay
111	South Florida Slash Pine

Since it has been artificially propagated far outside its natural range, slash pine can now be found in association with many other species.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Slash pine is monoecious and wind pollinated. Flowering begins at a relatively early age for conifers, usually between 10 and 15 years, but occasionally as early as 3 years *(2)*. Bisexual cones have been observed *(41)*. Open-grown trees that are fertilized and irrigated tend to flower at an early age. Similar treatments in close-spaced plantings do not result in earlier flowering. Mature scions grafted to seedling rootstocks begin flowering after 2 to 3 years and flower normally by 8 years if planted at wide spacings.

Early development of male strobili begins in June and continues for several weeks. Strobili become visible as small knobs near the base of vegetative buds in the fall. They usually occur in clusters of 12 or more, arranged spirally around the base of the current year's branches in the middle or lower crown. Further growth is delayed until midwinter. The staminate strobili are purple and 5 cm (2 in) long when pollen is shed in late January and February.

Development of female strobili begins between late August and mid-September. The female strobili are visible by December or January; they occur singly or in clusters and are most abundant on primary and secondary branches in the upper crown. They continue to grow until fully developed, by February in Florida and March further north. Female strobili are about 2.5 cm (1 in) long and red to purple at the time of pollination. They are receptive to pollen for a few days; receptivity of all strobili on a single tree may span a 2-week period. Outcrossing is normal because pollen shed and receptivity of female strobili occur at different times on the same tree. Selfing can occur under natural conditions and in seed orchards, but both yield of viable seed and vigor of trees produced is low.

Seed Production and Dissemination—Some seeds are produced each year, with good crops about every third year. In natural stands, cone production was increased by 50 to 100 percent after each of the following treatments: heavy thinning or crown release, stem injury, and fertilization applied before flower bud initiation. Wide initial spacing, fertilization, competition control, and irrigation are used to maintain a high level of production in seed orchards. Age, crown size, and genetic and environmental factors interact to influence seed production once a tree begins to bear cones.

Slash pine cones mature during September, approximately 20 months after pollination. There is a wide variation in time of cone maturation among trees, regions, and years. The specific gravity of cones with mature seeds is about 0.9 and they float in SAE 20 motor oil. Cones begin to open when the specific gravity decreases to 0.7. Natural seedfall occurs primarily in October but may be hastened by dry weather or delayed by wet weather. A few seeds may fall until March. Seed viability is increased if collected cones are stored several weeks before seeds are extracted.

There are 21,160 to 42,550 seeds per kilogram (9,600 to 19,300/lb) and the average is about 29,760/kg (13,500/lb) *(55)*. More than 90 percent of the winged seeds usually fall within 46 m (150 ft) of the parent tree. A slash pine plantation 13 to 16 years old, 15.2 m (50 ft) tall, grown initially at a spacing of 5.8 by 5.8 m (19 by 19 ft) or 297 stems per hectare (120/acre), will produce seeds at an average of 30.3 kg/ha (27 lb/acre) per year.

Seedling Development—Seed viability is usually good. Fresh seeds germinate rapidly, many within 2 weeks of natural seedfall if soil moisture is adequate. Those kept in cold storage for a year or more benefit from stratification *(38)*. Germination is epigeal *(55)*. Newly germinated seedlings have an average of 7.2 cotyledons, 30 mm (1.18 in) long. Hypocotyls average 37 mm (1.46 in) in length and 0.89 mm (0.035 in) in diameter. Seedlings in the cotyledon stage cannot be positively distinguished by external characteristics from those of loblolly *(Pinus taeda)* or Virginia *(P. virginiana)* pines *(37)*.

Seed size, which is quite variable, does not influence germination in the laboratory or nursery. Small seeds produce smaller seedlings than medium or large seeds, but field survival and average heights 1 to 2 years after field planting are similar for trees from seeds of all sizes.

Root development of seedlings is influenced by soil texture and structure. In one field study, taproot length was similar for first-year seedlings in all soils, but number of laterals and total length of all roots were largest on a clay, intermediate on a loam, and least on a sandy soil *(23)*. The presence of mycorrhizae has an important beneficial influence on survival and early growth of bare-root seedlings of all morphological grades *(24)*.

Juvenile trees past the seedling stage make from two to four height-growth flushes each year. The first begins when the winter bud elongates to become the spring shoot. Spring shoot growth begins slowly in February and gradually increases until it reaches a mean daily increment of about 7 mm (0.28 in) between mid-March and mid-April. Growth of this first shoot is completed by early June. First summer buds form in April, while the spring shoot is still growing, and second summer shoots are formed by the end of May. Winter buds are present in July and height growth is slow thereafter, although some growth may occur as late as October. The spring shoot makes up 62 percent and the summer shoots 38 percent of the annual height increment.

Height growth patterns may be influenced by silvicultural practices, previous land use, and competing vegetation. Site index curves for plantations on recently abandoned fields that were cultivated and fertilized are different from those for stands on areas formerly in timber and having a dense ground cover of brush or other low vegetation when planted to trees.

Radial growth begins in early February, about the same time as height growth, and continues throughout the summer and into October or November, as long as soil moisture is adequate. Root growth accelerates in early February, before terminal and radial activity begin. Root growth rates are fastest and the percentage of actively growing tips is highest in summer when soil moisture is optimum, but some root growth takes place during all seasons of the year.

Survival and early growth of seedlings are frequently stimulated by intensive site preparation treatments such as flat disking, chopping, or bedding. Disking and chopping are effective on deep, dry sandy soils where they control competing vegetation, incorporate organic matter into the topsoil, and may alter nutrient availability *(9)*. On sites with a shallow water table, bedding provides increased rooting space, improves aeration, and may increase growth *(39)*. Surface drainage may produce a similar response *(26)*. On droughty sites, weed control and irrigation may be effective *(1)*. Many slash pine sites are low in available phosphorus and nitrogen. Increased volume growth may result from fertilization with either element alone or a combination of both, depending on soil conditions *(20,43)*. Combinations of mechanical site treatment and fertilization may be more effective than either treatment alone *(1)*.

Vegetative Reproduction—Vegetative reproduction of slash pine rarely occurs naturally, but several techniques have been developed to reproduce specific individuals for use in seed orchards, clone banks, and genetic studies. Scions from mature trees are grafted onto seedling rootstocks in seed orchards and this is probably the most widely used technique of vegetative reproduction. The "cleft" graft is used with either succulent or dormant material. Normally, dormant scions are grafted onto stock plants just beginning active growth in early spring.

Air-layering (rooting undetached branches on young trees by girdling and treating them with a rooting hormone) has been more than 85 percent successful in some tests. Factors influencing results include age of the tree, concentration of the rooting hormone, season of treatment, and geographic location. Air layers usually develop a balanced root system and grow rapidly.

Cuttings from branches are difficult to root, especially those from older trees. There is considerable variation in results among trees, seasons, chemical treatments, and environmental factors. Enhanced carbon dioxide and a heated rooting medium greatly increase rooting. Needle fascicles can also be rooted, but the results are as poor and inconsistent as those with branch cuttings. In addition, most of the fascicles that form roots never begin height growth.

Sapling and Pole Stages to Maturity

Growth and Yield—Slash pine makes rapid volume growth at early ages and is adaptable to short rotations under intensive management. Yield tables have been available for natural stands since 1929 *(4,45,47,56)* and for plantations since 1955 *(13,21)*.

Stand basal area density has a strong influence on merchantable yield at any age (table 1). Also, almost three-fourths of the 50-year yield is produced by age 30, regardless of stand basal area.

Table 1—Estimated merchantable yields for unthinned natural stand of slash pine on average sites, 24.4 m (80 ft) at 50 years, by age and stand density[1]

	Yields at basal areas of		
Age	11.5 m²/ha or 50 ft²/acre	23.0 m²/ha or 100 ft²/acre	34.4 m²/ha or 150 ft²/acre
yr		*m³/ha*	
20	76.8	140.6	200.3
30	113.6	208.0	296.2
40	138.2	253.0	360.4
50	155.4	284.5	405.2
yr		*ft³/acre*	
20	1,097	2,008	2,861
30	1,623	2,971	4,232
40	1,974	3,614	5,148
50	2,220	4,064	5,789

[1] Adapted from Bennett (5). Yields are for volumes (outside bark) above a 15.2 cm (6 in) stump for trees 11.7 cm (4.6 in) in d.b.h. and larger to a 10.2 cm (4 in) diameter top outside bark.

Table 2—Estimated annual merchantable volume growth in thinned natural stands of slash pine on average sites, 24.4 m (80 ft) at 50 years, by age and stand density[1]

	Growth at basal areas of		
Age	11.5 m²/ha or 50 ft²/acre	23.0 m²/ha or 100 ft²/acre	34.4 m²/ha or 150 ft²/acre
yr		*m³/ha*	
20	7.98	10.50	11.41
30	6.23	7.56	7.49
40	5.04	5.74	5.25
50	4.13	4.55	3.92
yr		*ft³/acre*	
20	114	150	163
30	89	108	107
40	72	82	75
50	59	65	56

[1] Adapted from Bennett (5).

Current merchantable volume increment in thinned stands reaches a maximum rate before 20 years and declines thereafter (table 2). The instantaneous volume growth rate culminates at a high density in young stands and at progressively lower densities as age increases. Heavy thinning reduces periodic growth in young stands, but any density above 23 m²/ha (100 ft²/acre) at 20 to 30 years, or above 17 m²/ha (75 ft²/acre) at age 40, results in near-maximum volume growth.

Plantation yields are influenced by previous land use and interspecies competition, so there is wide variation in estimated wood production (table 3). Early yields are usually highest on recently abandoned fields where the young trees apparently benefit from the residual effects of tillage or fertilizer and the nearly complete lack of vegetative competition. Plantations established after the harvest of natural stands and without any site treatment other than burning generally have lower survival and, con-

Table 3—Range of estimated merchantable yields in unthinned slash pine plantations on average sites, 18.3m (60 ft) at 25 years, by age and number of surviving trees[1]

	Merchantable yield when surviving trees number		
Age	741/ha or 300/acre	988/ha or 400/acre	1235/ha or 500/acre
yr		*m³/ha*	
20	109.3 to 147.6	125.5 to 166.7	139.8 to 182.7
25	156.0 to 194.4	175.8 to 218.3	189.4 to 238.1
30	190.2 to 232.8	212.6 to 262.8	230.4 to 287.9
yr		*ft³/acre*	
20	1,562 to 2,109	1,793 to 2,382	1,997 to 2,610
25	2,228 to 2,777	2,511 to 3,118	2,706 to 3,402
30	2,717 to 3,325	3,037 to 3,754	3,291 to 4,113

[1] Adapted from Clutter and Dell *(10)*. Yields are for volumes outside bark above a 15.2 cm (6 in) stump for trees 11.7 cm (4.6 in) in d.b.h. and larger to a 10.2 cm (4 in) top diameter outside bark.

sequently, lower basal area and volume than stands on old fields *(13)*. Yields in plantations established after timber harvest and intensive site preparation such as disking or bedding are usually intermediate *(10)*.

Below age 30, maximum cubic volume yields are usually produced in unthinned plantations, so landowners seeking maximum yields on a short rotation will seldom find commercial thinning beneficial. Where sawtimber is the objective, commercial thinnings provide early returns while improving the growth and quality of the sawtimber and maintaining the stands in a vigorous and healthy condition *(11)* (fig. 2).

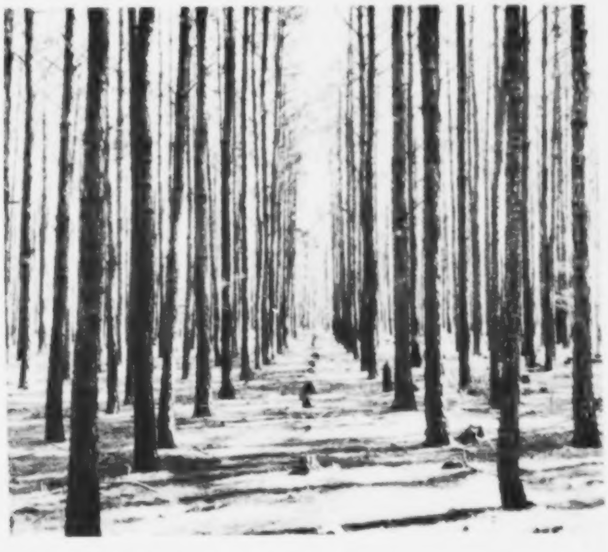

Figure 2—*A slash pine plantation after a commercial thinning in which every third row was harvested.*

Rooting Habit—Slash pine develops an extensive lateral root system and a moderate taproot. Maximum length of the lateral roots was more than double the tree height in three out of four site preparation treatments at 5 years. Taproots may be deformed as a result of poor planting technique, a restricting soil horizon, or a high water table *(46)*.

Reaction to Competition—Slash pine is relatively intolerant of competition and is classed as intolerant of shade. Stands protected from fires are invaded and replaced by more tolerant hardwood species. Unreleased seedlings established by direct seeding under a hardwood overstory seldom exceed 15 cm (6 in) in height the first year, while those freed from competition may reach 41 cm (16 in) *(38)*. Increased survival and growth of young trees on intensively prepared sites is attributed largely to the control of competing vegetation.

Because of this intolerance, even-aged management is usually recommended for slash pine *(21,33)*. Either the seed-tree or shelterwood system of natural regeneration may be used *(34)* (fig. 3). Exposed mineral soil is of primary importance in establishing natural regeneration. Overstory seed trees should be removed promptly after the new seedlings are well established. Failure to do so may retard growth in height, diameter, and merchantable volume of the next crop *(19)*. An alternative to natural regeneration is to clearcut and establish a new stand by planting or direct seeding.

Damaging Agents—The most serious disease of slash pine is fusiform rust caused by the fungus *Cronartium quercuum* f. sp. *fusiforme*. Most of the southern oaks serve as alternate hosts but the fungus damages only pines. Many trees are killed and others may become too deformed for high value products. Site treatments such as fertilization or vegetation control increase susceptibility to the disease. Resistance to the fungus is inherited, and attempts are being made to breed resistant strains.

Annosus root rot, caused by the fungus *Heterobasidion annosum*, is another serious disease of slash pine. It is most damaging on soils with good surface and internal drainage and is not a problem in flatwoods or shallow soils with heavy clay within 30 cm (12 in) of the surface. Infections begin when spores germinate on a fresh stump surface; the fungus then spreads to adjacent trees through root contacts. Diseased or dead and dying trees are usually found in groups.

Pitch canker, caused by the fungus *Fusarium moniliforme* var. *subglutinans*, causes heavy damage to slash pines in nurseries, seed orchards, and plantations. Cankers high in the crown may kill only the leader and a few laterals; the tree survives with a stem deformity and reduced growth. Cankers below the crown may eventually girdle the trunk and kill the tree (*8*).

The pales weevil (*Hylobius pales*) invades logging areas, feeds on the bark of seedlings, and may girdle the stem, causing wilting and eventual death. Small trees may be defoliated by the pine webworm (*Tetralopha robustella*), blackheaded pine sawfly (*Neodiprion excitans*), redheaded pine sawfly (*N. lecontei*), and Texas leafcutting ant (*Atta texana*). The black turpentine beetle (*Dendroctonus terebrans*) and engraver beetles (*Ips* spp.) can become problems. Slash pine is not particularly susceptible to injury by the southern pine beetle (*D. frontalis*) except where it is growing under environmental stress.

Other agents generally cause little damage, but some cause considerable losses under certain conditions. Senna seymeria (*Seymeria cassioides*) is one of a number of native root parasites that attack slash pine. Damage of economic importance is well documented but rare. Root rots may be a problem in tree nurseries or overmature stands. Red heart (*Phellinus pini*) is usually associated with mature or overmature timber and is not a problem in well-managed stands. Southern cone rust (*Cronartium strobilinum*) may destroy a cone crop and is particularly damaging in seed orchards as are several seed and cone insects (*17*).

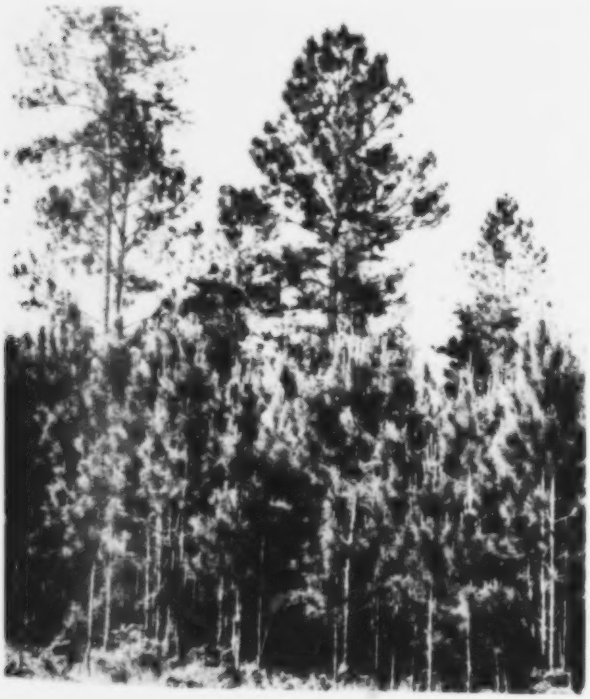

Figure 3—*Dense natural reproduction under a partial overstory of mature slash pines established by planting in central Louisiana.*

Young slash pines are susceptible to injury by wildfires until they are 3.0 to 4.6 m (10 to 15 ft) tall and the bark has thickened. Up to 50 percent of the needles may be scorched, but not consumed, with little mortality or growth loss.

Slash pine may suffer severe damage from glaze, particularly heavily thinned stands. It is subject to windthrow on shallow soils and wherever it does not develop a strong root system (*14*).

Special Uses

Slash pine is worked for naval stores. This industry, one of the oldest in the United States, has supplied a large portion of the resin and turpentine used throughout the world since colonial times. In many early forests, gum was the primary and sometimes the only product harvested. Chipping the trees for oleoresin increases bark thickness and reduces volume growth inside the bark 20 to 25 percent. A strain of inherently high-gum-yielding slash pine has been selected, and seedlings are commercially available in Florida and Georgia.

Cattle frequently graze the slash pine forests. Moderate grazing does little damage to trees past the seedling stage and may be indirectly beneficial by preventing the buildup of a dense and highly flammable understory.

Slash pine seeds are eaten by a variety of birds and small mammals. The dense foliage provides protective cover for many wildlife species during inclement weather. Slash pine may be planted to stabilize the soil on eroding slopes and strip mine spoil banks, where its rapid early growth is an advantage over slower growing species.

Genetics

Population Differences

Geographic variation among slash pine stands in different locations tends to be clinal due to a gradual change from a north temperate to a subtropical climate *(15)*. The variation among stands is less in the north than in the south.

Slash pine seeds from many sources have been grown in replicated provenance tests at several geographic locations *(51,57)*. When north Florida–south Georgia seed sources were planted north or west of their natural range they did not survive planting or grow as well as trees from South Carolina or Louisiana *(51)*. Trees from southern sources planted in the north do not grow or survive as well as those from northern sources *(28)*. In a northeast Florida plantation, all the trees broke bud at the same time, but trees grown from northern seed sources attained most of their growth early in the season, while trees from southern sources grew the most in the latter part of the season. The southern trees were never able to attain the growth of the northern trees *(3)*.

Seed source plantings outside the natural range of slash pine in South Carolina, western Louisiana, and central Mississippi have shown that trees from the southern part of the range are not well adapted to the more extreme northern and western environmental stresses of cold, ice, and extreme drought *(51,54)*.

A provenance test in western Louisiana showed that trees from seed sources in northeast Florida and south Georgia did not survive or grow as well in Louisiana as those from the western part of the slash pine range *(51)*. The most rapidly growing trees in east-to-west plantings came from seed sources in Georgia, western Florida, and southern Mississippi *(22)*.

Twelve morphological traits have been studied in cones, seeds, and foliage of five parent trees from each of 54 locations, and 13 traits have been studied in their seedlings *(52)*. The coefficients of variation tended to be highest for seedlings within mother trees and lower among stands and among mother trees within stands. Genetic variation among mother trees within stands was usually not much greater than stand-to-stand variation, suggesting that genetic gains are feasible through selection among stands as well as among individuals within stands.

The highest incidence of fusiform rust occurs among sources in southern Georgia, but no clear geographic patterns are apparent. There is also a strong interaction of seed source with site in the occurrence of fusiform rust *(22)*.

Races

South Florida slash pine (*Pinus elliottii* var. *densa* Little & Dorman) is a variety of slash pine found on about 121 410 ha (300,000 acres) *(48)* in the southern half of the peninsula of Florida *(21,32,35)*. It grows in pure stands on flatwood sites in the southern part of its range and on swampy or streamside sites in the northern part *(32)*. Where its range overlaps with the typical slash pine, there is a transition zone where morphological traits show clinal variation between the two varieties *(52)*. The range of South Florida slash pine also overlaps with that of longleaf pine (*P. palustris*) in transition zones between wet and dry sites, with longleaf more numerous on the drier sites *(32)*. South Florida slash pine is characterized by long needles, although they are not as long as those of longleaf, in fascicles of two, rarely three *(21)*; a thick needle hypodermus; 5 to 10 resin canals per needle *(58)*; thick branches with needles appearing clumped at the end; hard wood; whitish bud scales; a high specific gravity of 0.894, due to wide summerwood rings; and cones 20 percent smaller than typical slash pine *(27)*. The seedlings have a grass stage similar to longleaf pine and a thick taproot *(21)*. Mature trees have an irregular crown *(58)*.

Even-aged management, accomplished by leaving 15 to 25 trees per hectare (6 to 10 trees/acre) after a cut of 62 to 99 shelterwood trees per hectare (25 to 40/acre), appears to be the most successful silvicultural system for South Florida slash pine *(33,34)*. If a stand is clearcut, direct seeding in the fall will give the best stand *(40)*. Intensive site preparation is highly beneficial in reducing competition and available ground fuel. Problems with uneven-aged stand management include a lack of full stocking, fire hazard, since ground fuel accumulates when prescribed burning is prohibited, and root rot. Heavy thinning will give more sawtimber quickly, while light thinnings will give more total growth for pulpwood *(33)*.

When wildfires occurred in young stands, one-third of the surviving grass stage seedlings were observed to sprout from the root collar, but sprouts on the leader died back *(25)*. South Florida slash pine is more fire resistant than the typical variety in the seedling and sapling growth stages due to its thicker bark *(6,34)*. Controlled burns are possible when the trees are 3.7 to 4.6 m (12 to 15 ft) tall *(25)*.

South Florida slash pine was found to be superior to other southern yellow pines for wood properties except elasticity and shear parallel to the grain. This makes it an excellent timber for construction purposes *(42)*.

In its natural range, direct seeded South Florida slash pine will survive and grow as well as the typical variety but will not have as good survival and growth if nursery stock is planted *(6,40)*. For plantings, it is recommended that the typical variety be planted in the South Florida slash pine range using seed from Alachua County in northern Florida *(16)*. Height growth is better if seedlings are planted on beds *(21)*. Drought does not affect diameter growth of older trees, but excessive water will slow it down *(31)*.

Once height growth commences, South Florida slash pine has fewer insect and disease problems than the typical variety *(6)*. Pitch canker does affect this variety *(7)*, and as a grass stage seedling it is susceptible to brown spot *(Scirrhia acicola)*.

Site index curves and volume tables have been developed for South Florida slash pine *(29,30)*. With a site index of 15.2 m (50 ft) at base age 50 years the average d.b.h. of 1,112 trees per hectare (450/acre) at 20 years was 15 cm (6 in) with growth of 4.6 m^3/ha (65 ft^3/acre) per year.

Hybrids

Slash pine crosses naturally with the South Florida variety where their ranges meet and introgression has occurred among trees in the transition zone to the degree that it is difficult to distinguish between the two varieties *(52)*.

In areas where the natural distribution of slash pine overlaps that of the other pines, natural hybridization is usually precluded by phenology. Sand pine *(P. clausa)* is the earliest flowering pine and is followed by slash, longleaf, loblolly, and shortleaf *(P. echinata)* pines, the latter of which tend to shed pollen when slash pine strobili are no longer receptive. Late flowering sand pine or early flowering longleaf pine may hybridize with slash pine. Successful artificial hybridization depends on the choice of the female parent species as well as the particular individual of the species. There has been more successful sound seed produced in the slash × longleaf cross than in the reciprocal and no sound seeds were obtained in the sand × slash pine cross.

Slash pine has been artificially crossed with longleaf, loblolly, shortleaf, pitch *(P. rigida)*, and Caribbean *(P. caribaea)* pines. None of the offspring show potential hybrid vigor. The longleaf × slash hybrid shows the most potential because height growth begins quickly; it grows almost as fast as slash pine, self prunes well, is fairly resistant to both brown-spot needle disease and fusiform rust, and resembles longleaf pine in form and branching habit. On swampy sites in Australia there is some indication the Caribbean × slash hybrid progeny show superior yield to either parent alone. Slash × shortleaf hybrids have up to 16 percent dwarfs with some polyploids and mixoploids.

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Pinus flexilis James **Limber Pine**

Pinaceae **Pine family**

Robert Steele

Limber pine (*Pinus flexilis*), also known as white pine or Rocky Mountain white pine, is a long-lived, slow-growing tree of small to medium size. Its wood, light in weight, close-grained, and pale yellow, is used for rough construction, mine timbers, railroad ties, and poles. Its harvest is incidental to that of other, more desirable species.

Habitat

Native Range

Limber pine (fig. 1) grows from Alberta and southeastern British Columbia to New Mexico, Arizona, and eastern California. Notable outliers of this general distribution are found in the western portions of North Dakota, South Dakota, and Nebraska, and in eastern Oregon and southwestern California.

In the northern half of its distribution, limber pine is generally found near lower tree line and on dry sites in the montane forests. Between the 45th and 40th parallels, it grows in both lower and upper elevation forests and anywhere in between on dry, windswept sites (fig. 2). Its position gradually shifts upward in more southerly latitudes, so that in southern portions of its distribution, limber pine is more common from upper montane to alpine tree line, with only minor occurrences in the lower forested zones. Because of this adaptability, limber pine ranges in elevation from about 870 m (2,850 ft) in North Dakota *(29)* to about 3810 m (12,500 ft) in Colorado *(7)*.

Climate

Climatic data for actual limber pine habitat are quite scarce, but the general distribution of limber pine in Alberta, Montana, central Idaho, and east of the Continental Divide in Wyoming and Colorado, is in forested areas having a continental climate *(2,3)*. This climate is typified by a relatively small amount of precipitation, with the wettest months during the growing season, very low humidity, and wide annual and diurnal temperature ranges. Winter conditions may be very cold, but relatively dry, and often include rapid fluctuations in temperature associated with chinook winds. Notable exceptions to this distribution are the small populations in eastern Oregon and adjacent Idaho, which lie within the Pacific maritime influence *(3)*.

In the remainder of its distribution, limber pine grows in climates that tend to have either more evenly distributed yearly precipitation or a winter peak in precipitation along with summer convectional storms. Throughout its broad range, limber pine is mostly absent in areas strongly influenced by Pacific maritime weather patterns. Only at its southern limits in the mountains of eastern and southern California *(10)* does the pine encounter a strong pattern of proportionately high winter precipitation *(3* The amount of precipitation, however, is relatively smaller than that of the Pacific Northwest.

Soils and Topography

In some areas, limber pine grows in greater numbers on certain soils, but the relationships vary geographically. In general, the substrates are Entisols. In Montana, limber pine grows mainly on calcareous substrates *(26)*. Similarly, in eastern Idaho and western Wyoming, it grows mainly on soils derived from limestone or sandstone and is notably absent on adjacent granitic substrates *(34)*, yet the population in South Dakota grows on soils derived from granitic rock *(38)*. In central Idaho, limber pine is found largely on soils derived from sedimentary rocks; it is notably absent on granitic substrates, but grows in cracks of recent lava at Craters of the Moon National Monument *(33)*. In eastern Oregon, a recently discovered population is on soils derived from serpentine *(17)*. In Utah, it grows on soils developed from limestone, as on the Wasatch Plateau *(9)*, and on soils derived from quartzites, shales and limestones of the Uinta Range *(26)*. In southern Utah, it is most common on soils derived from sandstone and limestone *(44)*. In northeastern Nevada, it also grows on various calcareous substrates *(25)*, but in California, on substrates derived from granitic, obsidian, and pumice materials *(30)*.

Limber pine grows on a variety of topographies from gently rolling terrain to cliffs. It is most often found on rocky ridges and steep rocky slopes and can survive in extremely windswept areas at both lower and upper tree line.

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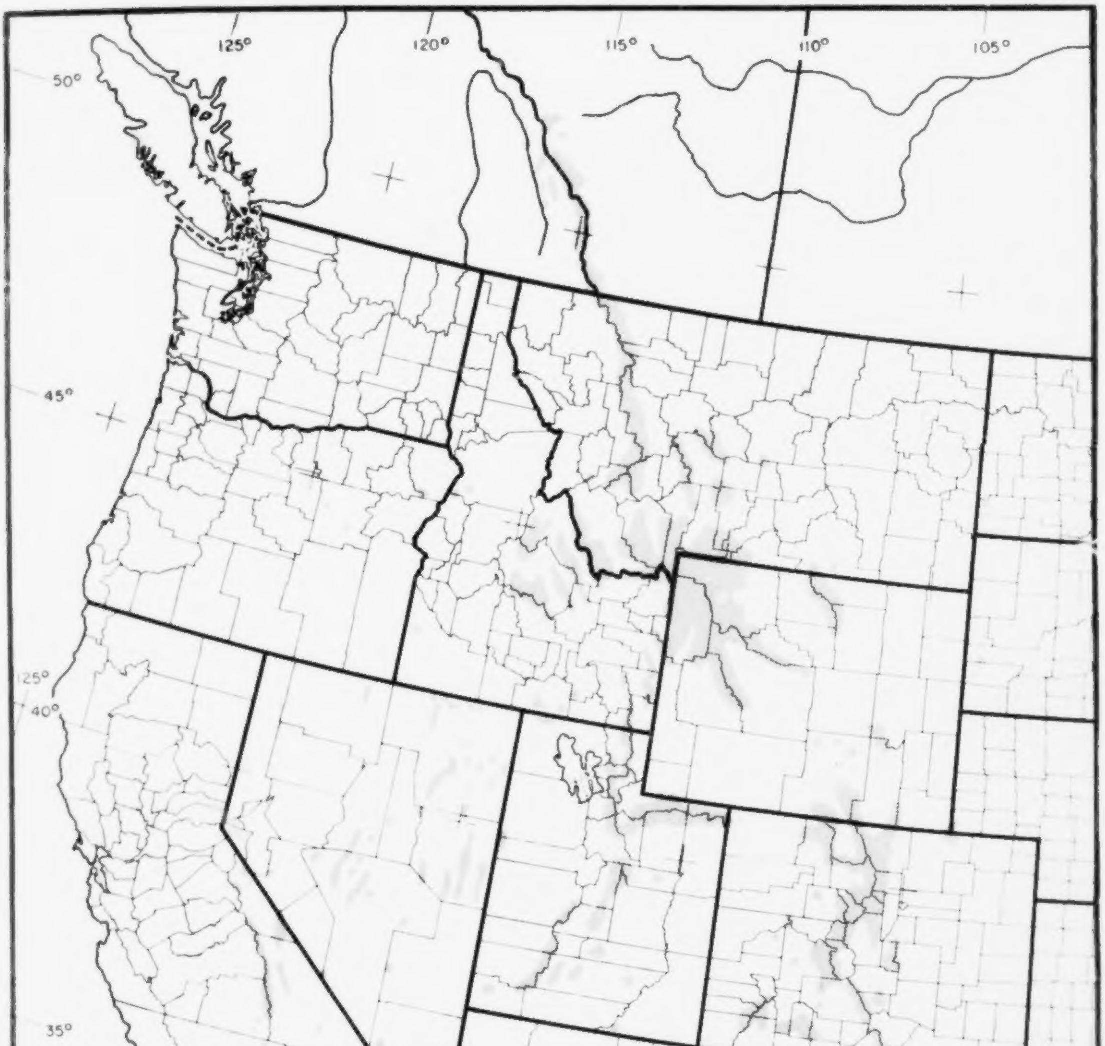
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Figure 1—*The native range of limber pine.*

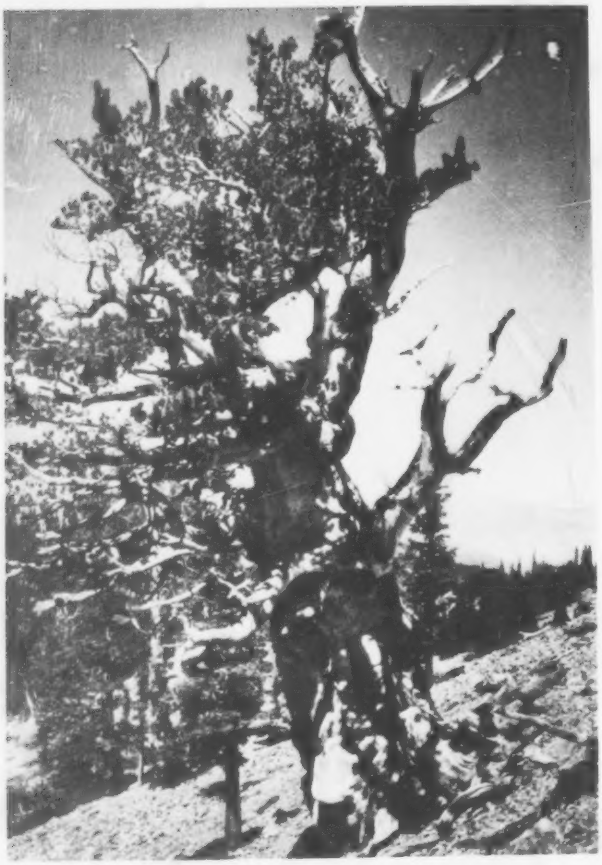

Figure 2—*A monarch limber pine at 2896 m (9,500 ft) in the Lost River Range of east central Idaho. The contorted branches, wind-sculptured bole, and barren site attest to the severe environments that this species can endure.*

Associated Forest Cover

As well as being dominant in the forest cover type Limber Pine (Society of American Foresters Type 219), limber pine is a minor component of the following *(32)*; Engelmann Spruce–Subalpine Fir (Type 206), Whitebark Pine (Type 208), Bristlecone Pine (Type 209), Interior Douglas-Fir (Type 210), Aspen (Type 217), Lodgepole Pine (Type 218), and Interior Ponderosa Pine (Type 237).

In Canada, Montana, and central Idaho, limber pine forms pure stands at lower tree line or mixes with Douglas-fir *(Pseudotsuga menziesii)*, and to a lesser extent, ponderosa pine *(Pinus ponderosa)* and Rocky Mountain juniper *(Juniperus scopulorum)*. It also appears as a minor component in stands of lodgepole pine *(Pinus contorta)*, Engelmann spruce *(Picea engelmannii)*, and occasionally subalpine fir *(Abies lasiocarpa)*. On some sites in Idaho and Montana, it is associated with whitebark pine *(Pinus albicaulis)*. In Canada, it is sometimes found with white spruce *(Picea glauca)*.

Southward into Wyoming, southern Idaho, and northern portions of Colorado, Utah, and Nevada, limber pine may dominate windswept slopes and ridges at upper or lower tree line or appear in stands of white fir *(Abies concolor)*, lodgepole pine, and Douglas-fir. In this region, limber pine appears most often with Engelmann spruce, subalpine fir, and quaking aspen *(Populus tremuloides)*, least often with ponderosa pine. In Wyoming, limber pine occasionally coexists with whitebark pine, particularly in the Wind River Range. The two species also coexist on a few sites in northeastern Nevada *(5,25)*, but usually where their ranges overlap they occupy different soils.

Farther south in the remainder of its range, limber pine forms open stands near upper tree line, both separately and with Great Basin bristlecone pine *(Pinus longaeva)* *(44)* but less often with Rocky Mountain bristlecone pine *(Pinus aristata)* *(6,18)*. It is also associated with whitebark pine on the east side of the Sierra Nevada *(4)*. Occasionally, it mixes as a minor seral species with subalpine fir and white fir *(23)*. Where limber pine would normally mix as a seral species with other conifers, as it does farther north, the closely related southwestern white pine *(Pinus strobiformis)* appears in these situations, but this species does not extend onto the dry windy sites where limber pine is climax *(23)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Limber pine is monoecious—male and female strobili are borne separately on the same tree. As with most pines, male strobili predominate in the lower crown and female strobili most often develop at the apical end of main branches in the upper crown. Male strobili emerge from buds in the spring and are arranged in small clusters of indistinct spirals. They may be green or yellow to reddish purple but turn brown when mature and about to shed their pollen. Pollen is shed during June and July. Female strobili emerge from buds shortly after the male strobili and are green or red to purple. Cone scales flex and they remain receptive to pollen for only a relatively short time during June and July. After pollination, scales close and the strobili begin to develop slowly.

Fertilization takes place in the spring or early summer, about 13 months after pollination. Cones and seeds mature rapidly following fertilization. As they mature, cones change color from green to lustrous yellow. They are light brown when mature in August and September. Seed dispersal takes place during September and October *(41)*.

Seed Production and Dissemination—Large seed crops are produced every 2 to 4 years and seed numbers generally range from 7,050 to 15,000/kg (3,200 to 6,800/lb) and average 10,800/kg (4,900/lb) *(38)*. Seed size varies geographically, with a tendency for increasingly larger seeds in more southerly latitudes *(14,36)*. Although some trees produce seed having an ineffective vestigial wing *(21)*, most limber pine seeds are wingless.

The seeds are disseminated largely by rodents and birds. Of the birds, Clark's nutcracker is most important; it can transport pine seed for at least 23 km (14 mi) from seed source to communal caching areas *(42)*. It can carry up to 125 limber pine seeds per trip in a sublingual pouch and buries in the ground one to five seeds per cache at a depth of 2 to 3 cm (0.8 to 1.2 in). Estimates indicate that Clark's nutcrackers cached in 1 year about 30,000 seeds per hectare (12,140/acre), most of which were limber pine *(22)*. The birds' preferred cache sites were windswept ridges and southerly aspects where snow does not accumulate and the ground is exposed early in the spring. The locations of most limber pine stands probably reflect the site preferences of dispersal agents rather than those of the pine, since its only other apparent means of dissemination is gravity.

Seedling Development—Germination is epigeal *(41)*. Like seed size, rate of seedling development depends on the geographic source. In one study *(36)*, 2-year-old nursery grown seedlings from Alberta averaged 4.3 cm (1.7 in), while those from New Mexico had reached 7.4 cm (2.9 in). Fall-sown seed, properly fertilized, produced a pencil-sized 2-0 seedling suitable for field planting *(14)*. In the wild, many seedlings develop in clusters from Clark's nutcracker seed caches *(20)*. The seedlings withstand this competition well and often retain the clumped habit into maturity.

Vegetative Reproduction—No information is currently available.

Sapling and Pole Stages to Maturity

Growth and Yield—The slow growth rate and poor form normally attributed to limber pine discourages commercial interest in its use for timber and there is little information regarding its growth and yield. There apparently has been no attempt, however, to plant this species on forest sites superior to those chosen by birds and rodents that cache the seed. Where occasional limber pines grow in more densely forested stands with other tree species, sapling and pole size trees are often straight and single stemmed. One study *(29)* suggests, however, that limber pine growth rates may be greater on exposed windy knolls than on warmer south slopes and more moist north slopes.

Rooting Habit—Type of substrate undoubtedly influences the rooting habit of limber pine. On many of the very rocky sites where it grows, the root system must follow the pattern of rock fracturing. As a result, most limber pine are quite wind firm. In nurseries, where there are better soil conditions, it develops a more uniform root system and can be transplanted by the ball and burlap method if previously root pruned *(7)*. Roots of limber pine are also known to associate with a mycorrhizal fungus *(Gomphidius smithii) (40)*.

Reaction to Competition—Limber pine is relatively intolerant of shade and therefore seral to most of its associated trees, the exceptions being quaking aspen, Rocky Mountain juniper, and possibly ponderosa pine. It is also considered seral to bristlecone pine and Douglas-fir but will codominate with these species on severe dry sites *(23)*. As a result, on most forest sites, limber pine normally acts as a pioneer species following fire or tree removal. Except on the most severe sites, where trees remain widely spaced, limber pine shows little evidence of maintaining its population in the presence of other conifers. It is most accurately classed as a species intolerant of shade.

Damaging Agents—Fire can easily kill young limber pines because of their thin bark. Fuel loads on most limber pine sites are too light, however, to generate severe fire damage, and most of the large trees normally survive. Porcupines feed on limber pine, especially in the winter months *(11)*. Several insects attack the pine in various ways. In Montana, the budworm *(Choristoneura lambertiana ponderosana)* feeds on the new needles of limber pine *(37)*. A cone moth *(Dioryctria* spp.) is presumed to have damaged limber pine seed in North Dakota *(29)*. In northern Idaho, the woolly aphid *(Pineus coloradensis)* attacked limber pine seedlings growing in test plots, but the pine showed considerable resistance to this insect *(16)*. Mountain pine beetle *(Dendroctonus ponderosae)* also occasionally attacks limber pine *(1)*.

Limber pine is susceptible to several major diseases. Spongy root and butt rot *(Armillaria mellea)* and the red-brown butt rot *(Phaeolus schweinitzii)* attack limber pine over much of its range. The crumbly brown cubical rot *(Fomitopsis pinicola)* and red ring rot *(Phellinus pini)* commonly cause heart rot in mature and damaged trees *(15,27)*. Limber pine is susceptible to white pine blister rust *(Cronartium ribicola)* and can suffer considerable mortality when susceptible species of the rust's alternate host *(Ribes)* are nearby. The limber pine dwarf mistletoe *(Arceuthobium cyanocarpum)* is a common parasite of this tree. Occasionally, lodgepole pine dwarf mistletoe *(A. americanum)* attacks limber pine, and the Douglas-fir dwarf mistletoe *(A. douglasii)* and southwestern dwarf mistletoe *(A. vaginatum* subsp. *cryptopodium)* occur as rare parasites *(12)*. Several foliage diseases also attack this tree, the most damaging being brown-felt snow mold *(Neopeckia coulteri) (15)*.

Special Uses

Limber pine is seldom sought for timber, but small quantities are occasionally harvested along with more desirable species. The wood has been used for rough construction, mine timbers, railroad ties, and poles *(2)*.

Although of marginal value for lumber, limber pine has other resource values. Its ability to grow on harsh sites often provides the only tree cover for wildlife. The large seeds are a nutritious food source for birds, rodents, and bears and were used as food by Native Americans and early pioneers *(20,21,29)*. In areas where timber is scarce, limber pine may be an important source of fuelwood. Increasing demands for fuelwood could deplete the accessible dead trees and eventually conflict with wildlife needs for shelter and nesting cavities.

Limber pine's abilities to withstand severe wind and dry site conditions are desirable shelterbelt traits, but its slow growth rate may discourage its selection for that purpose. Young trees, however, can withstand considerable bending, a necessary trait for reforestation of snow avalanche paths, and much of the pine's natural habitat lies within avalanche areas. Some limber pine habitats are also valuable watersheds, and as a pioneer species, the pine is a logical choice for initial site protection and for increasing snowpack *(39)*. The pine's characteristic branching pattern also adds to the esthetic appeal of the landscape, especially along ridge lines.

This tree's ability to endure very dry environments has allowed it to attain considerable age in some areas. One tree in southern California was found to be well over 1,000 years old *(13)*; another in central Idaho was 1,650 years old *(31)*. This feature makes limber pine a useful species in dendrochronologic studies.

Limber pine has potential as a Christmas tree, but its qualities are surpassed by southwestern white pine *(14,43)*. Seedlings from several seed sources have grown too slowly for economical Christmas tree operations but have ornamental value as dwarfed trees and even bonsai *(14)*. Some bonsai nurserymen also collect dwarfed limber pine from severe windy sites. As an ornamental, this species deserves more attention than current use would indicate. The ornamental trade has selected at least seven cultivated varieties: 'Columnaris'—a fastigiate form; 'Glauca' and 'Firmament'—both—with exceptionally bluish-green foliage; 'Glenmore'—with longer, more silvery foliage; 'Nana'—a dwarf bushy form; 'Pendula'—with pendulous branches; and 'Tiny Temple'—a low growing form *(7,19)*.

Genetics

Population Differences

Genetic variation exists within limber pine in a general north-south pattern, but the range of variability for any one trait is small. Some isolated populations in Wyoming, Nebraska, and Colorado appear to be more similar to those from more southern latitudes than to populations at the same latitude *(36)*.

Races

Three possible races of limber pine have been suggested, distinguished by height growth of the seedlings: (1) a northern race ranging from Alberta to north central Colorado and northern Utah and including the only sample from California; (2) a southeastern race that includes populations from the Wyoming–Nebraska border, east central Colorado, and north central New Mexico; and (3) a southwestern race in southern Utah and western Colorado (Nevada populations were not sampled) *(43)*. Further study, however, found no geographically associated patterns or trends when a much wider variety of characteristics was analyzed from the same seed sources *(36)*.

Hybrids

Although zones of intergradation between limber pine and southwestern white pine are found in north central Arizona and north central New Mexico *(36)*, no true hybrid populations of limber pine have been recorded. Limber pine has been crossed artificially with western white pine *(Pinus monticola)*, southwestern white pine *(P. strobiformis)*, Mexican white pine *(P. ayacahuite)*, Himalayan pine *(P. griffithii)*, eastern white pine *(P. strobus)*, and possibly whitebark pine *(P. albicaulis) (35)*.

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Pinus glabra Walt. Spruce Pine

Pinaceae Pine family

Susan V. Kossuth and J. L. Michael

Spruce pine (*Pinus glabra*), also called cedar pine, Walter pine, or bottom white pine, is a medium-sized tree that grows in limited numbers in swamps, river valleys, on hummocks, and along river banks of the southern Coastal Plain. Its wood is brittle, close-grained, nondurable, and is of limited commercial importance.

Habitat

Native Range

Although spruce pine (fig. 1) is considered a minor southern yellow pine species, it grows in a wide band across the South. It can be found on the low coastal areas from the valley of the lower Santee River in eastern South Carolina, south to the middle of northwest Florida, and west to the valley of Pearl River in eastern Louisiana *(14)*. The natural range lies between latitudes 29° to 33° N. and longitudes 78° to 91° W. *(2)*.

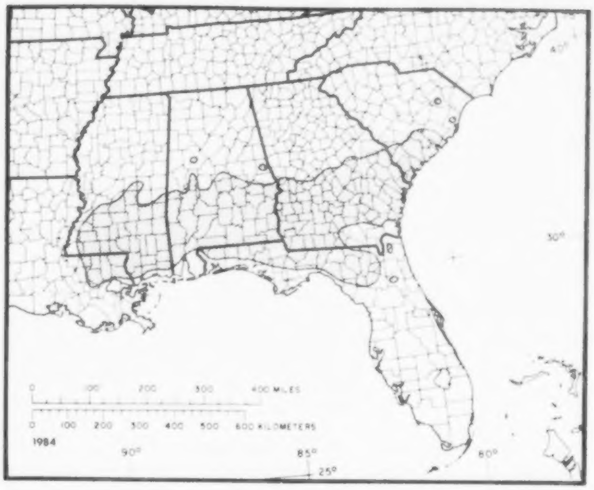

Figure 1—*The native range of spruce pine.*

Climate

In the Southeastern United States where spruce pine grows, the climate is characterized by long, hot, humid summers and mild winters. Annual rainfall is about 1270 mm (50 in), which is normally distributed about evenly throughout the year. Fall tends to be the driest season but summer droughts can occur. The growing season is about 240 days and the average annual temperature is 16° C (61° F).

Soils and Topography

Spruce pine grows on acidic sandy loam soils high in organic matter, intermediate between dry sandy soils and alluvial bottom land *(3)*. It grows well on poorly drained areas, often having a high water table, that are intermittently waterlogged, and may be found along stream banks or on rich moist hummocks *(6)*. These soils are most commonly found in the orders Spodosols and Entisols.

Associated Forest Cover

Spruce pine is not commonly found in pure stands. More often it is established in the shade of hardwoods such as magnolia (*Magnolia* spp.), gum (*Nyssa* spp.), hickory (*Carya* spp.), beech (*Fagus* spp.), and oak (*Quercus* spp.), where it may eventually overtop them. The forest cover types in which spruce pine is included *(5)* are Loblolly Pine–Shortleaf Pine (Society of American Foresters Type 80), Loblolly Pine (Type 81), Loblolly Pine–Hardwood (Type 82), Slash Pine (Type 84), and Slash Pine–Hardwood (Type 85). Other trees with which it is associated include pine (*Pinus* spp.), elm (*Ulmus* spp.), holly (*Ilex* spp.), cherry (*Prunus* spp.), hawthorn (*Crataegus* spp.), fringetree (*Chionanthus virginicus*), sweetgum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), pondcypress (*Taxodium distichum* var. *nutans*), loblolly-bay (*Gordonia lasianthus*), southern redcedar (*Juniperus silicicola*), flowering dogwood (*Cornus florida*), sourwood (*Oxydendrum arboreum*), redbay (*Persea borbonia*), and sweetleaf (*Symplocos tinctoria*). Shrubs and woody vine associates include beautyberry (*Callicarpa americana*), southern bayberry (*Myrica cerifera*), inkberry (*Ilex glabra*), sweet pepperbush (*Clethra alnifolia*), Alabama supplejack (*Berchemia scandens*), blueberry (*Vaccinium* spp.), poison-ivy

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(*Toxicodendron radicans*), greenbriar (*Smilax* spp.), blackberry (*Rubus* spp.), and grape (*Vitis* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Spruce pine trees generally begin producing cones by age 10. They are most prolific between the ages of 20 to 40 years *(14)*. The trees are monoecious, with pollen cones on weaker branches below the seed cones. First-year seed conelets appear in March in the northern parts of its distribution in Mississippi and somewhat earlier farther south.

Seed Production and Dissemination—Second-year cones mature during September and October and seeds are disseminated during November. When ripe, cones are green and have a specific gravity of 0.88. Test results show seeds are mature and germinable when the cones float in SAE 20-weight motor oil. Filled seeds sink in absolute ethanol, and empty or partially filled seeds float. Cleaned seeds are small, ranging from 88,180 to 114,640/kg (40,000 to 52,000/lb) and average 101,410/kg (46,000/lb). Seeds at a moisture content of between 5 and 10 percent have been stored for as long as 10 years at -17.8° to -15.0° C (0° to 5° F) and remained viable *(16)*.

Seedling Development—Seeds are not highly viable if the trees are isolated and poorly pollinated. Stratification improves seed germination *(11)*. Sixty percent germination can usually be attained after only 7 days of stratification at 4° C (39° F) *(3)*; however, the recommended cold stratification regime is 0.6° to 5.0° C (33° to 41° F) for 28 days *(16)*.

Germination is epigeal *(16)*. Seedlings develop well in shade of hardwoods and other pines, forming a wide-spreading, lateral taproot near the surface before penetrating deep into the soil *(14)*. When it invades old or cleared fields it may become established in the shade of loblolly and shortleaf pines *(10)*. Natural inoculation with mycorrhizae is highly beneficial to seedling establishment *(3)*.

Vegetative Reproduction—There is no published information on spruce pine vegetative reproduction. The species has been used experimentally as a rootstock for loblolly pine scions. Seed cone reproduction was greater when spruce pine was the rootstock than when loblolly pine was the rootstock *(15)*.

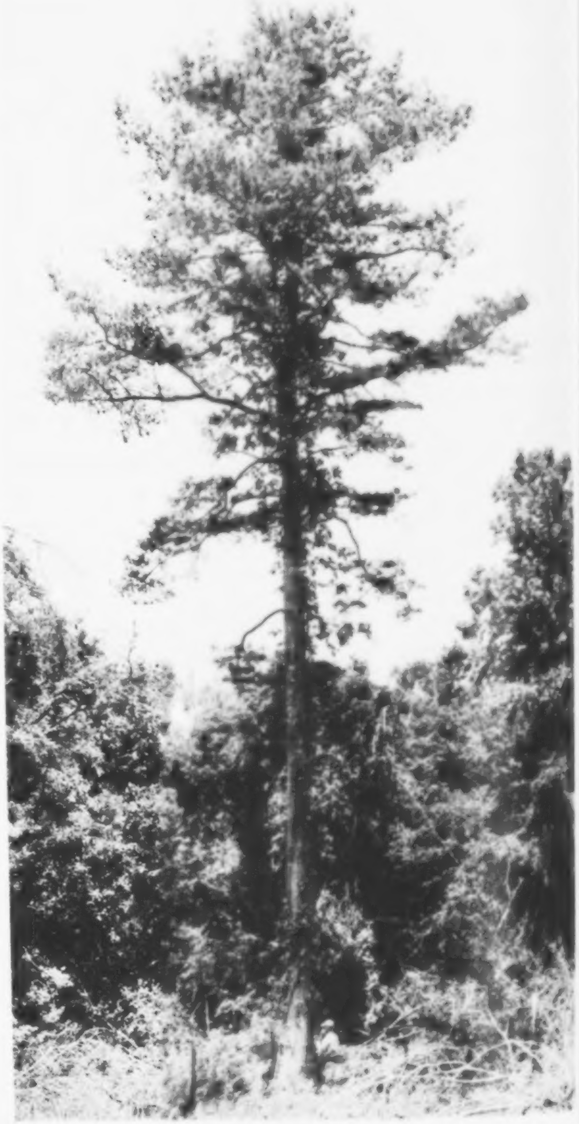

Figure 2—*A spruce pine 61 cm (24 in) in d.b.h. growing in a natural stand in Escambia County, FL.*

Sapling and Pole Stages to Maturity

Growth and Yield—Spruce pine (fig. 2) is one of the larger eastern North American pines, reaching a maximum of 38.1 m (125 ft) in height and 122 cm (48 in) in d.b.h. They are full grown at 60 to 75 years and as a scattered tree, often grow to a height of 27.4

to 30.5 m (90 to 100 ft) with a d.b.h. of 61 to 91 cm (24 to 36 in) *(8)*. The largest living spruce pine presently recorded measures 128 cm (50.3 in) in d.b.h. and 37.5 m (123 ft) in height. In a stand environment, spruce pine self-prunes to a height of 15.2 to 18.3 m (50 to 60 ft) *(14)*.

Its greatest commercial importance is in Louisiana, south Alabama, and Mississippi, where 80 percent of the standing volume is found *(18)*. Although it is not of great importance regionally, it can support a small, local forest industry. Some spruce pine has been planted on a small scale in South Carolina *(4)*. The volume of growing stock on commercial forest land is estimated at 13 131 000 m^3 (464 million ft^3) and the volume of sawtimber at 56 600 000 m^3 (2 billion ft^3).

Little growth and yield data are available, but estimates of different growth rates have been made on 12 trees in fast growth sites and 12 trees in slow ones within the natural range (table 1) *(8)*.

Rooting Habit—Spruce pine has a moderately deep taproot augmented by numerous moderately deep lateral roots.

Reaction to Competition—Little is known about spruce pine's ability to compete for minerals and water. Although it is classed as very shade tolerant, it is a slow grower under heavy competition. When planted with sweetgum and Shumard oak *(Q. shumardii)* on a bottom land site near Charleston, SC, spruce pine did not perform as well as sweetgum but grew slightly better than the Shumard oak. Seedling survival following the first growing season was similar for all three species (more than 90 percent), but by the end of five growing seasons, herbaceous vine and brush competition effects were reflected in overall survival and growth. Sweetgum had a 91 percent survival and grew best (4.1 m, 13.4 ft) on this site, while Shumard oak demonstrated higher survival than did spruce pine (72 percent vs. 48 percent) but did not grow as well (1.68 m vs. 2.38 m, 5.5 ft vs. 7.8 ft) *(19)*. Because of its shade tolerance, spruce pine may be able to compete successfully on cutover lands where other southern pines are unsuccessful *(9)*.

Table 1—Growth rate and age class for spruce pine *(8)*

Growth rate and age class	Growth rate	D.b.h.	Tree height
yr	*rings/cm*	*cm*	*m*
Slow			
15	3.3	12.4	11.6
30	3.7	17.0	15.4
45	3.7	26.9	20.6
Fast			
15	1.8	20.3	14.9
30	1.9	30.7	21.5
45	2.1	42.9	25.5
yr	*rings/in*	*in*	*ft*
Slow			
15	8.4	4.9	38.0
30	9.4	6.7	50.5
45	9.5	10.6	67.5
Fast			
15	4.6	8.0	49.0
30	4.8	12.1	70.5
45	5.3	16.9	83.5

Damaging Agents—Because spruce pine is usually found dispersed, it is less susceptible to insect and disease damage than are the other southern pines. It is immune to infection by *Cronartium quercuum* f. sp. *fusiforme (13)* and is only known to be susceptible to *Cronartium comandrae* when planted outside its native range. Similarly, the Nantucket pine tip moth *(Rhyacionia frustrana)*, can cause severe damage to spruce pine planted outside its range but is not considered a problem within its range *(17)*. A gall mite *(Trisetacus floridanus)*, attacks terminal shoots and causes the formation of galls and shortening of the shoot. No control is known for this insect.

Spruce pine at any age is highly susceptible to fire because of its thin bark (6.4 to 9.7 mm; 0.25 to 0.38 in). In the crown the bark is smooth and light gray, becoming darker with slightly irregular, shallow fissures with flat connecting ridges on mature boles. The ridges develop into small, closely appressed, light reddish brown scales. This finely furrowed bark is not at all plated like other southern pines but more closely resembles that of southern red oak.

Special Uses

Wood of this species is brittle and close-grained, has few resin canals, and is not durable *(14)*. The average shear strength parallel to the grain exceeds that of Douglas-fir *(Pseudotsuga menziesii)* and loblolly pine. Other structural features are similar to white fir *(Abies concolor)*. It is low in strength, with a specific gravity of 0.443 *(20)*.

The average fiber length is two-thirds of that of other southern pines but pulping characteristics are similar. It can be used as it occurs naturally for pulping operations, although use in large quantities for papermaking might require some operational changes to meet strength requirements *(9)*.

Spruce pine responds to treatment with paraquat by producing lightwood, that is, wood soaked with oleoresin. Its response is similar to that of slash pine, and the increase in turpentine produced is proportionately greater than the increase in resin acids *(12)*.

Spruce pine is planted to some extent for use as a Christmas tree. Productivity is about half that of the more popular Virginia pine, and two shearings per growing season are a necessity in southeastern Louisiana *(7)*.

As a member of mixed pine–hardwood communities it provides some habitat and food for wildlife.

Genetics

Wood specific gravity showed no trends in any of the four compass directions over the range. A few trees on plots near the Atlantic and Gulf Coasts had higher specific gravities (0.44 to 0.50) than did those inland (0.40 to 0.46) *(20)*.

Spruce pine has been successfully crossed with shortleaf pine but only when the latter was the female parent *(1)*. No natural hybrids have been reported.

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Pinus jeffreyi Grev. & Balf. **Jeffrey Pine**

Pinaceae **Pine family**

James L. Jenkinson

Jeffrey pine (*Pinus jeffreyi*) was discovered in 1852 in the Shasta Valley of California by John Jeffrey, a Scottish botanical explorer. Partly overlapping ponderosa pine (*Pinus ponderosa*) in range and superficially resembling it, Jeffrey pine was first classified as a variety of ponderosa pine *(28,45)*. These western yellow pines produce wood of identical structure and quality and are closely related taxonomically *(10)*. Jeffrey pine is distinct chemically, ecologically, and physiologically and is readily distinguished from ponderosa pine on the basis of bark, leader, needle, bud, and cone morphology *(23)*.

Habitat

Native Range

Primarily a California species, Jeffrey pine (figs. 1,2) ranges north through the Klamath Mountains into southwestern Oregon, across the Sierra Nevada into western Nevada, and south in the Transverse and Peninsular Ranges into northern Baja California *(10,20)*. This distribution is intimately linked with edaphic factors in the northwest portion of the range and strongly reflects climatic and elevational factors in the northeast, central, and southern portions.

Jeffrey pine thrives in comparatively harsh environments throughout most of its range *(1,21,24,55,58)*. Contrasted with ponderosa pine, Jeffrey pine completes annual top growth sooner, enters dormancy earlier, and requires longer cold exposure for leader growth in spring *(27)*. Because Jeffrey pine is especially cold hardy *(21,22)*, tolerant of drought *(51,58,59)*, and adapted to short growing seasons, it competes well and typically dominates other conifers on cold, xeric, and infertile sites.

Climate

Jeffrey pine grows well in diverse temperature regimes. Cold winters largely distinguish its range east of the Sierra–Cascade crest from that in the Klamath Mountains, western Sierra Nevada, and southern California. Most populations east of the crest are exposed to January mean minima between -13° and -5° C (8° and 23° F), while those in the west and south are between -7° and 2° C (19° and 36° F). Summer nights are warmer and differences in day–night temperatures are smaller for Jeffrey pine in the western Sierra Nevada and southern California than elsewhere in the range. July day–night differences in these regions are as little as 11° C (20° F), and rarely exceed 19° C (34° F). In the Klamath Mountains and east of the Sierra–Cascade crest, July day–night differences mostly exceed 19° C (34° F), approach 26° C (47° F) in some areas, and decrease to 13° C (24° F) only for stands at highest elevations.

Throughout the range, precipitation falls mostly during the winter season. Mean annual rainfall averages as little as 380 to 430 mm (15 to 17 in) in places east of the Sierra–Cascade crest, is only 200 mm (8 in) for certain stands scattered along the eastern Sierra Nevada and Virginia Range of western Nevada *(3)*, and exceeds 1270 to 1520 mm (50 to 60 in) in parts of the western Sierra Nevada and Klamath Mountains. Mean snowfall in Jeffrey pine localities typically ranges from 30 cm (12 in) or less at lowest elevations in the Klamath Mountains to well over 520 cm (204 in) at high elevations in the Sierra Nevada, particularly along the central crest.

Soils and Topography

Perhaps one-fifth of the distribution of Jeffrey pine is on ultramafic soils. At middle elevations on the western slope of the northern Sierra Nevada and in the North Coast Range and Klamath Mountains, Jeffrey pine often dominates and is almost entirely restricted to soils derived from ultramafic rocks--peridotites and their alteration products, serpentinites. The typical forest soils formed on such rocks are fine, fine loamy, and clayey texture skeletal surface soils. On these highly infertile, mostly shallow soils, Jeffrey pine descends to low elevations: 490 m (1,600 ft) in Butte County, 260 m (850 ft) in Humboldt County, 60 m (200 ft) in Del Norte County, CA, and 183 m (600 ft) in Douglas County, OR. The only native Jeffrey pine in California's South Coast Range grows on an isolated mass of sterile serpentine in San Benito County *(19)*. Jeffrey pine's innately short growing season, limited nutrient and water demands, and extensive root growth probably ensure its presence on poor sites.

Above 1600 m (5,250 ft) in ultramafic regions and at all elevations everywhere else within its range, Jeffrey pine grows on any well-drained forest soil, regardless of parent material. Most of the usual soils that carry Jeffrey pine are coarse or gravelly sandy

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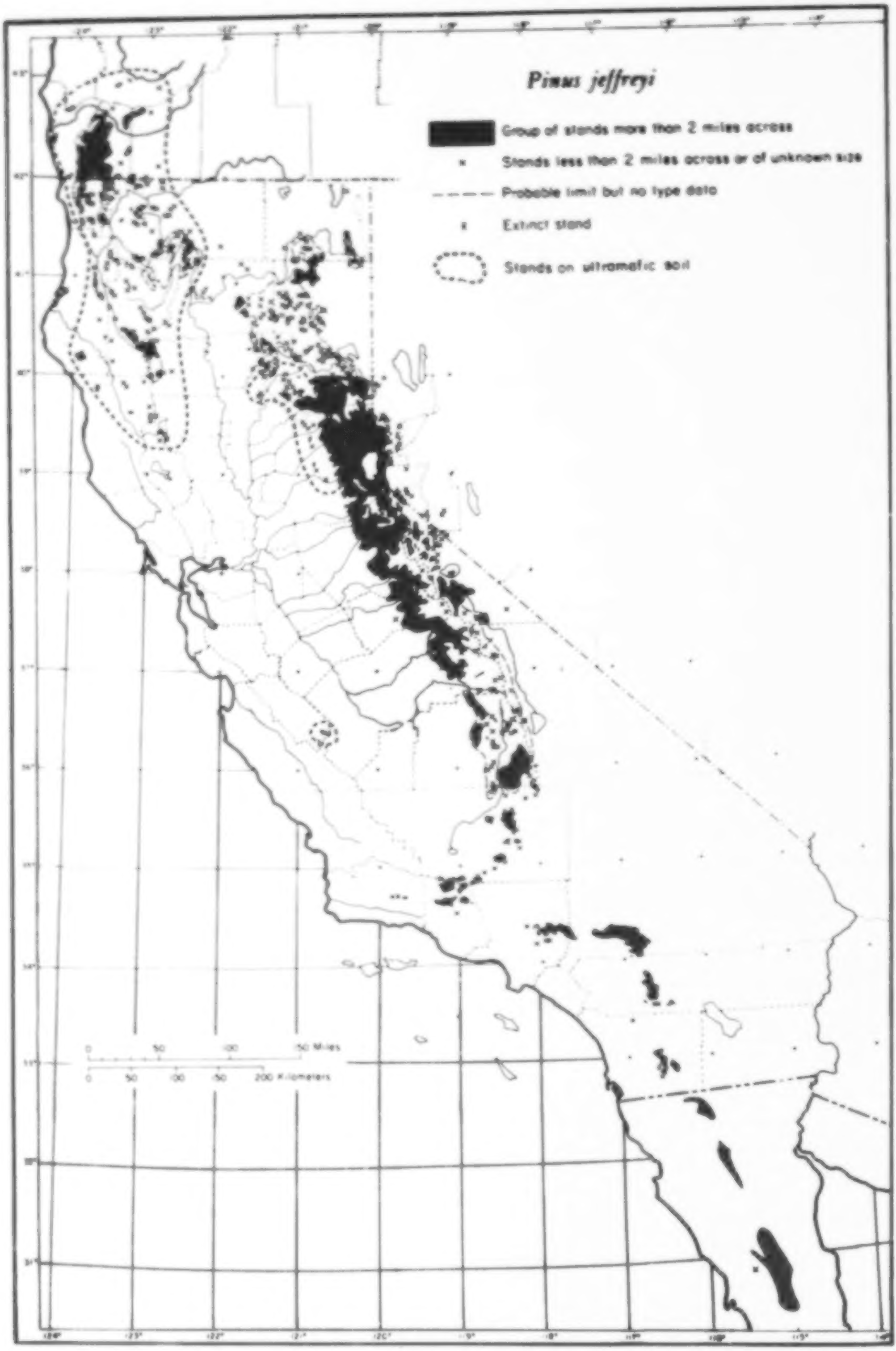
Pinus jeffreyi
Group of stands more than 2 miles across
Stands less than 2 miles across or of unknown size
Probable limit but no type data
Extinct stand
Stands on ultramafic soil
0 50 100 150 Miles
0 50 100 150 200 Kilometers

Figure 1—*The native range of Jeffrey pine.*

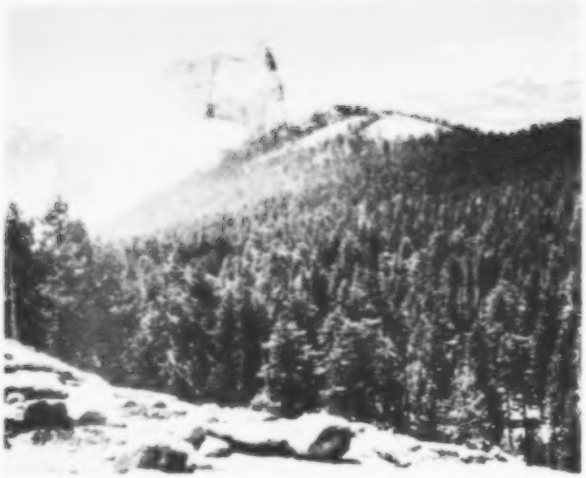

Figure 2—*A virgin Jeffrey pine forest near Half Dome, Yosemite National Park in the western Sierra Nevada, in 1916.*

loams or loamy coarse sands that often merge with rocklands. Where these soils are of recent volcanic origin (ashes, pumice, or cinders) they are Dystric or Typic Xerorthents or Xeropsamments of the order Entisols. Jeffrey pine characteristically grows on granitic soils in the Sierra Nevada (fig. 2). These soils extend over complex systems of branching ridges, ravines, and canyons at elevations ranging from 1520 to 2740 m (5,000 to 9,000 ft), are usually found in a humid microthermal climate, and vary from about 0.6 to 1.4 m (2 to 5 ft) deep. They are Dystric and Typic Xerochrepts and Xerumbrepts of the order Inceptisols. Volcanic soils and mud flows commonly support Jeffrey pine in the northern Sierra Nevada and adjacent Cascade Range. They are extensive on gentle to steep slopes of dissected plateau-like areas at elevations up to 1830 m (6,000 ft), and most vary from 0.5 to 1 m (1.6 to 3.3 ft) deep *(31)*. They are Ultic, Typic, and Dystric Haploxeralfs of the order Alfisols.

East of the Sierra Nevada crest from Lassen to Alpine Counties, CA, and along the Virginia Range of adjacent western Nevada, isolated patches of Jeffrey and ponderosa pines grow on more than 125 islands of altered andesite *(3)*. These edaphically restricted stands range in elevation from 1310 to 2130 m (4,300 to 7,000 ft), and many are within the Pinyon-Juniper woodland *(20)*.

Associated Forest Cover

Incense-cedar *(Libocedrus decurrens)* is the most widespread associate of Jeffrey pine on ultramafic soils. Locally prominent are Douglas-fir *(Pseudotsuga menziesii)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, ponderosa pine, sugar pine *(Pinus lambertiana)*, western white pine *(P. monticola)*, knob-cone pine *(P. attenuata)*, Digger pine *(P. sabiniana)*, and Sargent cypress *(Cupressus sargentii)*. Above 1600 m (5,250 ft) in the Klamath Mountains, North Coast Range, and northern Sierra Nevada, Jeffrey pine shares various soils and sites with California red fir *(Abies magnifica)*, white fir *(A. concolor)*, sugar pine, incense-cedar, western white pine, and Sierra lodgepole pine *(Pinus contorta* var. *murrayana)*.

South of the Pit River in northeastern California and on the east side of the Cascade Range in southwestern Oregon and northern California, Jeffrey and ponderosa pines form extensive forests and usually intermingle in both closed and open, parklike stands. Jeffrey pine forests range widely from 1520 to 2130 m (5,000 to 7,000 ft) of elevation in the northern Sierra Nevada, and from 1830 to 2900 m (6,000 to 9,500 ft) in the central and southern Sierra Nevada. Ponderosa pine, sugar pine, white fir, incense-cedar, California red fir, western white pine, lodgepole pine, and western juniper *(Juniperus occidentalis)* all mix in locally, but few of them join Jeffrey pine on south slopes and granitic soils *(9,44)*.

Jeffrey pine is the dominant yellow pine in forests east of the Sierra Nevada crest and in the Transverse and Peninsular Ranges into Baja California. In the Sierra San Pedro Martir, it ranges from 1830 to 3050 m (6,000 to 10,000 ft) and shares the southern limits of sugar pine, white fir, incense-cedar, and lodgepole pine *(10,45,52)*.

Jeffrey pine forests constitute one of the more unusual forest cover types in western North America *(14)*. Because Jeffrey pine has wide edaphic and elevational ranges in diverse physiographic regions, Jeffrey Pine (Society of American Foresters Type 247) is highly variable and adjoins or merges with many others: Red Fir (Type 207), White Fir (Type 211), Lodgepole Pine (Type 218), Pacific Douglas-Fir (Type 229), Port-Orford-Cedar (Type 231), Douglas-Fir–Tanoak–Pacific Madrone (Type 234), Interior Ponderosa Pine (Type 237), Western Juniper (Type 238), Pinyon–Juniper (Type 239), Sierra Nevada Mixed Conifer (Type 243), Pacific Ponderosa Pine–Douglas-Fir (Type 244), Knob-cone Pine (Type 248), Canyon Live Oak (Type 249), and California Mixed Subalpine (Type 256). Associated understory species are diverse, reflecting climatic influences *(14*, p. 123).

Life History

Our present understanding of Jeffrey pine's life history is probably limited, because most studies have concentrated on populations in northern California.

Reproduction and Early Growth

Flowering and Fruiting—In California, Jeffrey pine flowers in June or July, depending on the climatic region, elevation, aspect, and annual variation in temperature *(12)*. The species is monoecious. Female strobili emerge from the bud shortly after the male strobili. After pollination, the conelets develop slowly, reaching less than one-fifth the size of mature cones the first growing season. Fertilization occurs about 13 months after pollination, and the cones grow rapidly to reach full size in summer of the second season.

Unripe cones are pale or dark purple to black and shade to light brown or dull purple at maturity. Seeds are mature when cone specific gravity (fresh weight basis) drops to between 0.81 and 0.86; they are safely collected in stands where one or two trees have cones that are cracking, with seed scales separating. Mature cones are usually 13 to 23 cm (5 to 9 in) long, open to resemble old-fashioned straw beehives or skeps, and normally shed most of their seeds in September or October *(30)*.

Seed Production and Dissemination—Although trees as young as 8 years have borne a cone crop, typical cone-bearing Jeffrey pines are 18 to 55 m (60 to 180 ft) tall and produce a large seed crop every 2 to 8 years *(30)*.

When shed, the winged seeds drop about 2.2 m/s (7.2 ft/s) *(49)*, indicating that winds of 8 km/h (5 mi/h) carry them no further than the height of seedfall. Seeds can be widely spread, however. Fall storms are common in California's mountains, and winds average 13 to 26 km/h (8 to 16 mi/h) in September and October. Gusts occasionally exceed 64 to 113 km/h (40 to 70 mi/h), enough to blow seeds up to 15 times the height of seedfall, even 750 m (2,460 ft) from a tree height of 50 m (164 ft).

Besides wind, certain seed eaters also disseminate seeds. In the Sierra Nevada, Clark's nutcracker harvests and stores substantial quantities of ripe Jeffrey pine seeds, burying them in many small clusters in a wide variety of microsites, and often where snow accumulates least and melts rapidly in spring *(54)*. At least eight other common birds also extract and eat seeds of Jeffrey pine.

Several kinds of squirrels cut and store large quantities of Jeffrey cones for their seeds, including the widespread golden-mantled ground squirrel and western gray squirrel. The chickaree cuts whole cones and buries them in the ground, and chipmunks harvest seeds by gnawing cones in the tree. Mice and voles efficiently gather, cache, and consume large quantities of shed seed.

Like seeds of most pines in temperate climates, Jeffrey pine germinates quickly the spring after seedfall. For starting new stands after harvest, however, natural regeneration is seldom quick and never reliable (fig. 3). The usual cause of failure is vegetation in the original understory that simply preempts the site. Irregular seed crops, poor seed dissemination, seed predators, cutworms, pathogens, mammals, and drought are also lethal factors *(16,25)*.

Seedling Development—Mature seeds show highly variable degrees of dormancy after air drying and cold storage. Different seed sources require different amounts of moist, cold stratification for rapid and complete germination *(30)*. Although certain sources east of the Sierra–Cascade crest may not require pretreatment, stored seeds of most sources germinate best after 60 days of stratification.

In forest tree nurseries in northern California and southern Oregon, seeds are sown in April to utilize the full growing season. Germination is epigeal *(30)*. Stratified seeds are sown above a maximum depth of 6 to 8 mm (0.25 to 0.30 in) and at a density to produce 269 to 323 seedlings per square meter (25 to 30/ft^2). Fertilization and irrigation regimes are

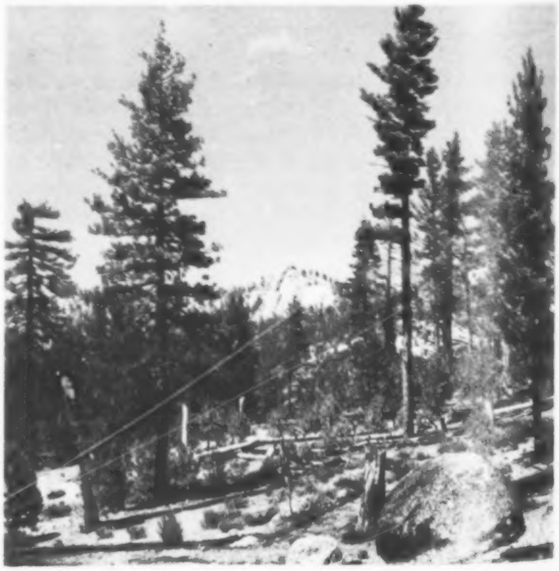

Figure 3—*Natural regeneration of Jeffrey pine in a beetle-killed stand near Lloyd Meadow, Sequoia National Park, in the southern Sierra Nevada. (1937 photo by J. E. Patterson)*

tailored to seedling requirements in the particular nursery soil and climate. For most sources west of the Sierra–Cascade crest and in southern California, seedlings of plantable size are raised in one growing season. For many sources east of the crest, seedlings are often carried through two seasons.

To consistently raise large and healthy seedlings of Jeffrey pine, nursery soil management is crucial. In midsummer, dry, fallow soil is ripped deeply enough to restore rapid drainage and aeration, and then fumigated. Fumigation is necessary to control nematodes, root rots such as *Rhizoctonia, Phytophthora, Pythium, Macrophomina*, and *Fusarium* spp., and foliar diseases such as *Phoma* and *Sirococcus (38)*.

Jeffrey pine is quickly established in the field when dormant seedlings are lifted from nursery beds at the right time in winter, held in cold storage, planted at the right time in spring, and protected against animal damage and competing vegetation. Lifted seedlings are root-pruned 23 cm (9 in) below the cotyledon scars and stored in polyethylene-lined bags at 1° C (34° F). Planting starts at the onset of spring conditions, when soils warm sufficiently to permit water uptake and root growth. Planting is ideally completed before the last spring rain to ensure that roots will be sealed in the soil. In the Sierra Nevada, field survivals of 90 to 99 percent are attainable on cleared sites within the species' elevational range *(27)*.

Vegetative Reproduction—Jeffrey pine does not sprout.

Sapling and Pole Stages to Maturity

Growth and Yield—In field plantations, Jeffrey pine grows less rapidly than ponderosa pine during the sapling stage, but more rapidly in the pole stage. Jeffrey pine has trailed ponderosa pine in height growth through more than 5 years in the northern Sierra Nevada in Plumas County, CA *(15)*, 6 years in the Warner Mountains in Modoc County, CA *(35)*, and 11 years in the western Sierra Nevada in Stanislaus County, CA (table 1).

After 5 years in the Plumas test, every stock class of Jeffrey pine gradually overtook its ponderosa counterpart, averaging 127 cm (50 in) tall and exceeding ponderosa pine by 5 percent 9 years after planting *(15)*. In the Stanislaus plantation, Jeffrey pine accelerated growth into the pole stage, increasing height by one-fourth at 10 years, and at 20 years had nearly overtaken ponderosa pine in both height and diameter (table 1). Leader length at 20 years was 14 percent greater for Jeffrey pine, indicating that the species' difference might soon be eliminated. In the Modoc plantation, trees averaged 5 m (16.5 ft) tall and 15 cm (6 in) in diameter when thinned at 30 years *(34,35)*. At thinning and for the next 15 years, the growth of these poles was apparently the same for both species. When seedlings of Jeffrey and ponderosa pines from the Sierra Nevada were planted at 560 m (1,830 ft) in the North Coast Range in Mendocino County, CA, the Jeffrey pines outgrew ponderosa pines from comparable elevations, edging them in both height and diameter in 17 years *(6)*.

Jeffrey pine may live 400 to 500 years and on the best sites can reach an impressive size. Trees larger than 152 cm (60 in) in d.b.h. were often measured in virgin forests east and west of the Sierra–Cascade crest (fig. 4). The largest known survivor is on the Stanislaus National Forest in the western Sierra Nevada and measures 229 cm (90 in) in diameter and 53 m (175 ft) tall *(36)*. Yellow pines taller than 61 m (200 ft) are recorded in early volume table measurements, and some of them probably are Jeffrey pine *(24)*.

Several general accounts state that Jeffrey pines 1.2 to 1.8 m (4 to 6 ft) in diameter and 52 to 61 m (170 to 200 ft) tall were typical of the species' best growth on deep, coarse-textured and well-drained soils *(28,45,52)*. Stands of similar description may still be seen in the high country of Yosemite National Park. By contrast, stand productivity is low for Jeffrey pine on ultramafic soils. Dunning's site index (base age 300 years) may often be as high as 29 m (95 ft), but the typical stocking capacity is just 11 to 28 percent of normal basal area *(33)*.

Yield data have never been acquired specifically for Jeffrey pine, but Jeffrey pine apparently grows to the

Table 1—Growth of Jeffrey pine and ponderosa pine in the Tuolumne River watershed of the western Sierra Nevada[1]

Species	Plantation age	Tree height	Stem diameter	Leader length	Height increase
	yr	*m*	*cm*	*m*	*pct*
Jeffrey pine	11	2.15	4.3	0.41	26
	20	7.05	16.2	0.56	9
Ponderosa pine	11	3.64	8.9	0.43	13
	20	7.19	17.8	0.49	7
	yr	*ft*	*in*	*ft*	*pct*
Jeffrey pine	11	7.1	1.7	1.4	26
	20	23.1	6.4	1.8	9
Ponderosa pine	11	11.9	3.5	1.4	13
	20	23.6	7.0	1.6	7

[1] Seedlings were planted on cleared sites at an elevation of about [illegible]

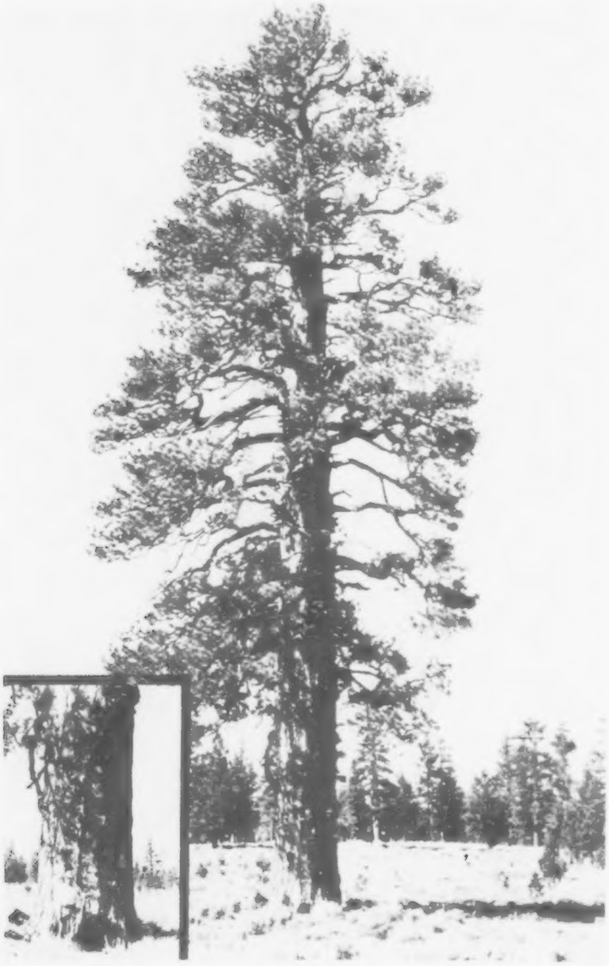

Figure 4—*An immense Jeffrey pine (213 cm; 83.9 in d.b.h.) near Last Chance Creek, Plumas National Forest, in the eastern Sierra Nevada. (1944 photo by J. E. Patterson)*

same age and maximum size as ponderosa pine. Observations in mature natural stands bolster the belief that yield data for ponderosa pine can be confidently applied to pure stands of Jeffrey pine, or to Jeffrey pine mixed with ponderosa pine *(24,25)*.

Rooting Habit—Windthrow is rare for Jeffrey pine. Surveys of windthrow sales indicate that Jeffrey pine is seldom included and is highly windfirm compared with its timber associates. In juvenile through mature stages, Jeffrey pine typically has a deep taproot. The primary lateral roots are strong and extensive, some growing horizontally and others angling downward. Such root systems apparently adjust well to the physical and chemical environments encountered. In an open stand of Jeffrey pine on a shallow ultramafic soil in the northern Sierra Nevada, live roots up to 5 cm (2 in) in diameter were encountered in soil pits up to 30 m (100 ft) away from the nearest trees, at distances greater than tree height.

Reaction to Competition—Jeffrey pine occasionally regenerates beneath open, overmature stands, but growth is checked until the overstory is removed. The species is intolerant of shade, and root competition from old-growth trees is intense. In such circumstances, saplings 40 or more years old and less than 1 m (3 ft) tall are common. After release, suppressed saplings take 3 to 7 years to extend root systems, produce efficient crowns, and begin rapid height growth *(24)*.

As a result of wildfire, stagnated sapling stands of naturally regenerated Jeffrey and ponderosa pines are common in the 1.6 million ha (4 million acres) of yellow pine forests in northeastern California. Densities have sometimes reached 42,000 stems per hectare (17,000/acre). Growth is so slow that stand development virtually ceases, yet dominants and codominants can respond to thinning. In one 55-year-old stand with 27,200 stems per hectare (11,000/acre), thinning 2.5-m (8.2-ft) tall saplings to a spacing of 2.7 m (9 ft) tripled their periodic radial growth and increased height growth 67 percent in 5 years, compared with unthinned controls *(53)*.

Survival and growth of planted Jeffrey pine reflects the thoroughness of site preparation and post-planting protection against aggressive understory plants *(42,43)*. Heavy invasion of any vegetation soon after planting makes seedling survival unlikely, if not impossible. Brush, grasses, and sedges all are lethal competition for available soil water in Jeffrey pine's dry summer environments, and many shrub species quickly overtop and markedly slow the growth of surviving seedlings.

Low vegetation even reduces the growth of established Jeffrey pine. In northeastern California removing perennial bunchgrass and sedge, alone or together with sagebrush *(Artemisia tridentata)* and bitterbrush *(Purshia tridentata)*, increased the mean 5-year basal area increment of pine poles by as much as 38 percent *(18)*.

Damaging Agents—Extremely low temperatures can kill needles, buds, last season's shoots, and even the inner bark of Jeffrey pine. East of the Sierra Nevada crest, winter minima between −35° and −43° C (−31° and −45° F) have extensively damaged Jeffrey pine. Trees whose inner bark was destroyed by freezing were killed *(56)*. Jeffrey pine may also undergo severe physiological drought and foliar damage in winter, when sunny and warm or windy days desiccate needles of trees rooted in soils that are too cold for adequate water uptake. Jeffrey pine is highly sensitive to anaerobic conditions and is killed outright when root systems are flooded by beaver ponds or new stream channels or are buried under fill from land grading operations *(2)*.

Human activity is often damaging in other ways. Highway de-icing salts *(48)*, sewage effluents *(2)*, and air pollutants such as ozone *(39)* all may severely injure or kill Jeffrey pine. Like other conifers, Jeffrey pine is susceptible to herbicide damage at certain seasons of the year and stages of growth *(40)*. Spraying during the growing season may kill trees or distort growth of new shoots, although observations in plantations suggest that Jeffrey pine resists phenoxy herbicide damage.

Among the biotic agents attacking Jeffrey pine are two needle diseases, a limb canker, at least five different rusts, western dwarf mistletoe, three major root diseases, and various heart rots *(2)*.

Elytroderma disease *(Elytroderma deformans)* has reached epidemic proportions in stands into which cold air drains and has reduced growth and killed trees for years after major outbreaks *(46)*. Medusa needle blight *(Davisomycella medusa)* has markedly decreased growth of individual trees, especially on poor sites after drought. Cenangium limb canker *(Cenangium ferruginosum)* may severely attack young trees growing under poor conditions and usually kills suppressed or weakened branches.

Stalactiform rust *(Peridermium stalactiforme)* infects lower limbs and spreads upward in the crowns of young Jeffrey pine; infected trees are almost always near the alternate hosts, particularly *Castilleja* spp. Filamentosum rust *(Peridermium filamentosum)* kills the middle or upper crowns of scattered mature trees, can spread from pine to pine, and has displayed a potential for intense outbreaks. Sweetfern rust *(Cronartium comptoniae)* frequently kills young trees, and tarweed rust *(Coleosporium madiae)* may cause heavy defoliation in occasional wet years. Western gall rust *(Peridermium harknessii)* kills seedlings and large trees of Jeffrey pine by producing abundant, globose branch galls or large bole-deforming stem cankers. Although its major outbreaks are often decades apart, this rust is ubiquitous in California and potentially hazardous to young Jeffrey pine in moderately cool, humid environments *(2)*.

The worst disease of Jeffrey pine is caused by western dwarf mistletoe *(Arceuthobium campylopodum)*. Heavy infections cause witches' brooms, severely reduce growth, and eventually kill the tree. Young trees are highly susceptible to infection from surrounding infected overstory trees *(37)*. Dwarf mistletoe has predisposed many stands to insect attack and has induced 60 to 80 percent of all Jeffrey pine mortality in years of severe drought *(4)*.

Fungal diseases of the roots of Jeffrey pine include annosus *(Heterobasidion annosum)*, armillaria *(Armillaria mellea)*, and black stain *(Verticicladiella wagnerii)*. Fungi that cause heart rots in Jeffrey pine include species of *Lentinus*, *Fomes*, and *Polyporus*. In southern California, red rot *(Dichomitus squalens)* attacks Jeffrey pine through broken tops, bole wounds, and large dead limbs *(2)*.

Insects that damage Jeffrey pine are as numerous as the fungal diseases. Collectively attacking every part of the tree, they include twig and needle scales, various defoliators, borers, and tip moths, several bark beetles, and a host of cone and seed feeders *(17)*.

The ponderosa pine twig scale *(Matsucoccus bisetosus)* feeds on branches and stems of trees of all ages and is the most destructive of the scales. Two of the more serious defoliators are the pine needle sheathminer *(Zelleria haimbachi)* and pandora moth *(Coloradia pandora)*. Larvae of the sheathminer have destroyed more than 75 percent of the new needles in localized outbreaks in California. Larvae of the pandora moth are among the largest of any forest insect and consume whole needles in spring before bud break. Extensive outbreaks occur every 20 to 30 years, cause heavy defoliation for 2 to 4 years, and predispose the trees to attack by bark beetles and borers.

The western pineshoot borer *(Eucosma sonomana)* stunts the needles and retards height growth of young trees by as much as 30 percent annually. The ponderosa pine tip moth *(Rhyacionia zozana)* kills current shoots of saplings and young trees up to 2 m (6 ft) tall and may chronically retard growth for many years. The fir coneworm *(Dioryctria abietivorella)* kills the terminal buds of saplings and poles and frequently causes a permanent fork in the main stem. Larvae of the pine reproduction weevil *(Cylindrocopturus eatoni)* can destroy saplings and young trees where brush competition causes severe water stress.

The Jeffrey pine beetle *(Dendroctonus jeffreyi)* is the single worst enemy of Jeffrey pine *(13)*. This bark beetle is prevalent throughout the range of its host, and has caused staggering losses of timber in mature stands. Several other insects that attack the main stem commonly precede or accompany Jeffrey pine beetle, notably the California flatheaded borer *(Melanophila californica)* and two pine engravers, the emarginate ips *(Ips emarginatus)* and Oregon pine engraver *(I. pini,* or *I. oregonis).* The red turpentine beetle *(Dendroctonus valens)* also attacks injured or weakened Jeffrey pine and induces fatal attacks by other bark beetles. Throughout California, lethal bark beetle activity is usually associated with dwarf mistletoe infestation or root rots, indicating that pathogens predispose the trees to insect attacks *(4).*

Insects often cause major losses of Jeffrey pine cones and seeds. The worst of these are the Jeffrey pine seedworm *(Laspeyresia injectiva)* and ponderosa pine seedworm *(L. piperana),* which eat seeds within the immature cone *(17,26).*

Deer, jack rabbits and snowshoe hares, pocket gophers, porcupines, and domestic livestock damage and kill young Jeffrey pine. Resident, mobile populations of these mammals make substantial losses likely in most areas. Pocket gophers consume whole seedlings, feed on the roots, stem, and crown of saplings, and often annihilate young plantations *(11).* Porcupines commonly eat the inner bark and cambium of saplings and poles and either kill them outright or cause a spiketop above the girdled stem.

Special Uses

In commerce, no distinction is made between the wood of Jeffrey pine and that of ponderosa pine.

Genetics

Jeffrey pine is genetically variable. Estimates of the average number of alleles and average heterozygosity per enzyme locus show its allelic variation is high *(7).*

Population Differences

Jeffrey pine displays large differences in seedling and sapling growth, and in most nurseries seed source largely determines seedling size. When raised in a nursery in the western Sierra Nevada, dormant seedlings of Jeffrey pine from east of the Sierra Nevada crest develop top growth capacity earlier in winter than sources from the western Sierra and southern California. At the same time, seedlings of all sources from east of the crest and southern California show two separate peaks in root growth capacity: November and January for the eastern Sierra, and December and February or March for southern California. The depression between peaks can be deep or shallow and span 1 or 2 months. By contrast, seedlings from ultramafic soil in the western Sierra show a single peak in midwinter *(27).*

Growth in young plantations markedly depends on seed source. In the North Coast Range, stem volumes of 20-year-old Jeffrey pine from five sources in the northern Sierra Nevada differed by up to twofold *(6).* Trees with least growth were from seed parents near 2230 m (7,300 ft), and those with most growth from parents on ultramafic soil near 1050 m (3,450 ft). Trees from parents at the highest elevation, at 2510 m (8,235 ft) near the Sierra crest, were notably larger than trees from 1770, 1920, and 2230 m (5,800, 6,300, and 7,300 ft).

In the western Sierra Nevada, performance of 20-year-old Jeffrey pine improved with the match between seed source and planting site elevation *(5).* At low elevations, trees from 1050 m (3,450 ft) were taller and had less stem taper than trees from 2400 m (7,860 ft). At high elevations, mortality was 30 percent in the low elevation source, as against 2 percent in high elevation sources. Trees of high elevation sources were 1.1 to 1.6 m (3.6 to 5.2 ft) taller, and fewer than 10 percent suffered breaks in the main stem, compared with 27 percent in the low elevation source.

Data at hand are not sufficient to describe the rangewide pattern of genetic variation in the growth of Jeffrey pine. Definitive data are probably years away, because early growth of Jeffrey pine depends on specific interactions between the seed source and planting site environment. Until rotation-age tests of particular sources on specific sites indicate otherwise. planting any Jeffrey pine of a nonlocal source is unwise. Nonlocal sources are probably maladapted, yet may not show it until sometime during or after the pole stage.

There is good evidence that some Jeffrey pine may be resistant to dwarf mistletoe infection *(47,57).*

Hybrids

In certain stands, Jeffrey pine is known to hybridize with ponderosa pine *(23)* and Coulter pine *(60),* but most mixed stands contain no morphological evidence of genetic intermingling. Natural hybrids are rare because these pines differ substantially in flowering time *(12)* and cross only with difficulty *(8).*

Under controlled conditions, Jeffrey pine will cross with either ponderosa pine or Coulter pine *(32,41),* but crossability is very low in either combination. With Jeffrey pine as the female parent, 40 percent of the strobili dusted with ponderosa pollen may produce cones, and 3 percent of the seeds may be sound; with Coulter pollen, the expected percentages are 61 and 3 *(8).* Observed crossing barriers include failure of viable pollen to germinate on the nucellus, failure of pollen tubes to maintain normal growth rates in the nucellus, lack of exact timing between tube growth and egg formation, collapse of the proembryo, and failure of the embryo to develop. In both crosses, slow growth of the pollen tube appears to be the most common barrier to development of hybrid seeds *(29)*.

Although hybrids of Jeffrey and ponderosa pines are rare in the upper Mixed Conifer Forest and in sympatric distributions east of the Sierra–Cascade crest, hybrids may be locally common on ultramafic soils in the western Sierra Nevada. Of 13 mature Jeffrey pines sampled on an ultramafic soil in Sierra County, CA, 12 had the expected 95 to 99 percent heptane, but one had 75 percent heptane and 7 to 8 percent each of alpha-pinene, beta-pinene, and limonene, which indicate ponderosa pine ancestry *(50)*. Beneath overstories of Jeffrey pine on ultramafic soil in Placer County, CA, individual saplings and poles show a diverse mix of morphological traits, suggesting that the pollen parents were ponderosa pines growing on the same soil or in mixed conifer forests nearby.

Capitalizing on Coulter pine's immunity to the pine reproduction weevil, the Forest Service produced backcrosses of Jeffrey–Coulter hybrids to Jeffrey pine on a large scale for many years *(8)*. The weevil is controllable silviculturally, however, and in recent years the demand for backcross seedlings has ceased.

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Pinus lambertiana Dougl. Sugar Pine

Pinaceae Pine family

Bohun B. Kinloch, Jr. and William H. Scheuner

Called "the most princely of the genus" by its discoverer, David Douglas, sugar pine *(Pinus lambertiana)* is the tallest and largest of all pines, commonly reaching heights of 53 to 61 m (175 to 200 ft) and d.b.h. of 91 to 152 cm (36 to 60 in). Old trees occasionally exceed 500 years and, among associated species, are second only to giant sequoia in volume. For products requiring large, clear pieces or high dimensional stability, sugar pine's soft, even-grained, satin-textured wood is unsurpassed in quality and value. The huge, asymmetrical branches high in the crowns of veteran trees, bent at their tips with long, pendulous cones, easily identify sugar pine, which "more than any other tree gives beauty and distinction to the Sierran forest" *(25)*.

Habitat

Native Range

Sugar pine (fig. 1) extends from the west slope of the Cascade Range in north central Oregon to the Sierra San Pedro Martir in Baja California (approximate latitude 30° 30′ to 45° 10′ N.). Its distribution is almost continuous through the Klamath and Siskiyou Mountains and on west slopes of the Cascade Range and Sierra Nevada, but smaller and more disjunct populations are found in the Coast Ranges of southern Oregon and California, Transverse and Peninsula Ranges of southern California, and east of the Cascade and Sierra Nevada crests. Its southern extremity is an isolated population high on a plateau in the Sierra San Pedro Martir in Baja California. Over 80 percent of the growing stock is in California *(49)* where the most extensive and dense populations are found in mixed conifer forests on the west slope of the Sierra Nevada.

In elevation, sugar pine ranges from near sea level in the Coast Ranges to more than 3000 m (10,000 ft) in the Transverse Range.

Elevational limits increase with decreasing latitude, with typical ranges as follows:

Cascade Range	335 to 1645 m (1,100 to 5,400 ft
Sierra Nevada	610 to 2285 m (2,000 to 7,500 ft
Transverse and Peninsula Ranges	1220 to 3000 m (4,000 to 10,000 ft
Sierra San Pedro Martir	2150 to 2775 m (7,056 to 9,100 ft

Climate

Temperature and precipitation vary widely throughout the range of sugar pine. For equivalent latitudes, temperature decreases and precipitation increases with elevation, and for equivalent elevations, temperature increases and precipitation decreases from north to south. Patterns unifying this variability are relatively warm, dry summers and cool, wet winters. Precipitation during July and August is usually less than 25 mm (1 in) per month, and summertime relative humidities are low. Although water stored in snowpacks and soils delays the onset and shortens the duration of summer drought, evaporative stress often becomes great enough to arrest growth in the middle of the season *(15)*. Most precipitation occurs between November and April, as much as two-thirds of it in the form of snow at middle and upper elevations *(26)*. Within its natural range, precipitation varies from about 840 to 1750 mm (33 to 69 in). Because winter temperatures are relatively mild and seldom below freezing during the day, considerable photosynthesis and assimilation are possible during the dormant season, at least partially offsetting the effects of summer drought *(15)*.

Soils and Topography

Sugar pine grows naturally over a wide range of soil conditions typically associated with conifer-hardwood forests. Soil parent materials include rocks of volcanic, granitic, and sedimentary origin and their metamorphic equivalents and are usually not of critical importance. Soils formed on ultrabasic intrusive igneous rocks such as peridotite and serpentinite, however, have low calcium-to-magnesium ratios and usually support open conifer stands of inferior growth and quality. Nevertheless, sugar pine is often the dominant conifer on the more mesic of these sites *(39,40)*.

Because site productivity is a function of several environmental variables—edaphic, climatic, and biotic—it is difficult to relate parent material groups or particular soil series with specific productivity

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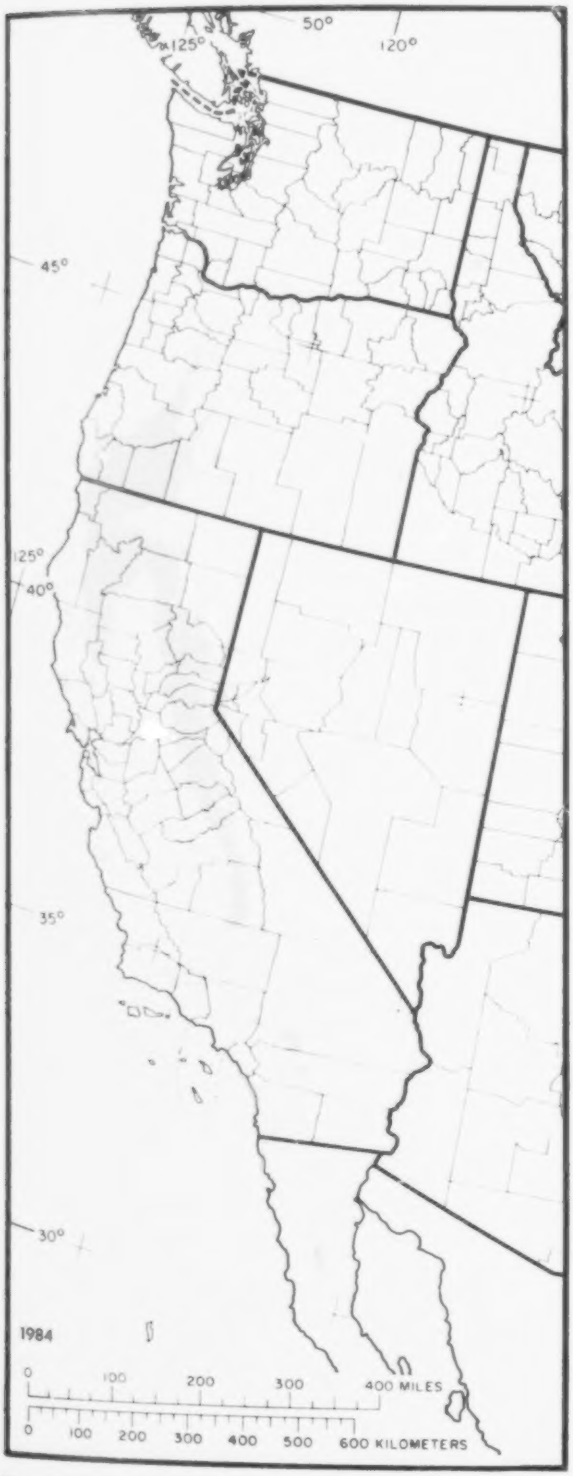

Figure 1—*The native range of sugar pine.*

classes, especially when they span wide ranges of elevation and latitude. Other factors being equal, the main edaphic influences on conifer growth are soil depth and texture, permeability, chemical characteristics, and drainage and runoff properties *(5)*.

The most extensive soils supporting sugar pine are well drained, moderately to rapidly permeable, and acid in reaction. Soils derived from ultrabasic rocks are very slightly acid to neutral (pH 7.0). In general, acidity increases with soil depth. Several edaphic properties are influenced by the degree of soil profile development. Soil porosity, permeability, and infiltration rate decrease with more developed profiles, while water-holding capacity, rate of run-off, and vulnerability to compaction increase.

Sugar pine reaches its best development and highest density on mesic soils of medium textures (sandy loam to clay loams) but ranges into the lower reaches of frigid soils when other climatic variables are suitable. These soils are found most commonly in the order Ultisols and Alfisols. The best stands in the Sierra Nevada grow on deep, sandy loam soils developed from granitic rock. In the southern Cascade Range the best stands are on deep clay loams developed on basalt and rhyolite. In the Coast Range and Siskiyou Mountains in California and Oregon, the best stands are on soils derived from sandstone and shale.

Much of the terrain occupied by sugar pine is steep and rugged. Sugar pines are equally distributed on all aspects at lower elevations but grow best on warm exposures (southern and western) as elevation increases. Optimal growth occurs on gentle terrain at middle elevations.

Associated Forest Cover

Sugar pine is a major timber species at middle elevations in the Klamath and Siskiyou Mountains, Cascade, Sierra Nevada, Transverse, and Peninsula Ranges. Rarely forming pure stands, it grows singly or in small groups of trees. It is the main component in the forest cover type Sierra Nevada Mixed Conifer (Society of American Foresters Type 243) *(10)* generally comprising 5 to 25 percent of the stocking. It is a minor component in 10 other types:

207	Red Fir
211	White Fir
229	Pacific Douglas-Fir
231	Port-Orford-Cedar
232	Redwood
234	Douglas-Fir–Tanoak–Pacific Madrone
244	Pacific Ponderosa Pine–Douglas-Fir
246	California Black Oak
247	Jeffrey Pine

249 Canyon Live Oak

In the northern part of its range, sugar pine is commonly associated with Douglas-fir *(Pseudotsuga menziesii)*, ponderosa pine *(Pinus ponderosa)*, grand fir *(Abies grandis)*, incense-cedar *(Calocedrus decurrens)*, western hemlock *(Tsuga heterophylla)*, western redcedar *(Thuja plicata)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, tanoak *(Lithocarpus densiflorus)*, and Pacific madrone *(Arbutus menziesii)*. In the central part it is associated with ponderosa pine, Jeffrey pine *(Pinus jeffreyi)*, white fir *(Abies concolor)*, incense-cedar, California red fir *(A. magnifica)*, giant sequoia *(Sequoiadendron giganteum)*, and California black oak *(Quercus kelloggii)*. Farther south, the usual associates are Jeffrey pine, ponderosa pine, Coulter pine *(Pinus coulteri)*, incense-cedar, white fir, and bigcone Douglas-fir *(Pseudotsuga macrocarpa)*. At upper elevations Jeffrey pine, western white pine *(Pinus monticola)*, California red fir, and lodgepole pine *(P. contorta)* grow with sugar pine. In the Sierra San Pedro Martir, Jeffrey pine and white fir are the main associates.

Common brush species beneath sugar pine include greenleaf manzanita *(Arctostaphylos patula)*, deerbrush *(Ceanothus integerrimus)*, snowbrush *(C. velutinus)*, mountain whitethorn *(C. cordulatus)*, squawcarpet *(C. prostratus)*, bearclover *(Chamaebatia foliolosa)*, bush chinkapin *(Castanopsis sempervirens)*, bitter cherry *(Prunus emarginata)*, salal *(Gaultheria shallon)*, coast rhododendron *(Rhododendron californicum)*, and gooseberries and currants in the genus *Ribes (11)*. From a silvicultural standpoint, *Ribes* spp. are especially important because they are alternate hosts to the white pine blister rust fungus *(Cronartium ribicola)*. At least 19 different species grow in the Mixed Conifer Type, of which the Sierra gooseberry *(Ribes roezlii)* is most prevalent on more xeric, upland sites, and the Sierra currant *(R. nevadense)* on more mesic sites *(35)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Sugar pine is monoecious. Reproductive buds are set in July and August but are not discernible until late in the next spring. Time of pollination ranges from late May to early August, depending on elevation, and to a lesser extent on latitude.

Female strobili are 2.5 to 5.0 cm (1 to 2 in) long at time of pollination and double in size by the end of the growing season. Fertilization of eggs by male gametes takes place late the following spring, about 12 months after pollination. By this time, the seed is at its final size with a fully developed coat. Conelet elongation continues during the second season until maturation in late summer. Mature sugar pine cones (fig. 2) are among the largest of all conifers, averaging 30 cm (12 in) and ranging up to 56 cm (22 in) long. Dates of cone opening range from mid-August at low elevations to early October at high elevations *(12,19,32)*.

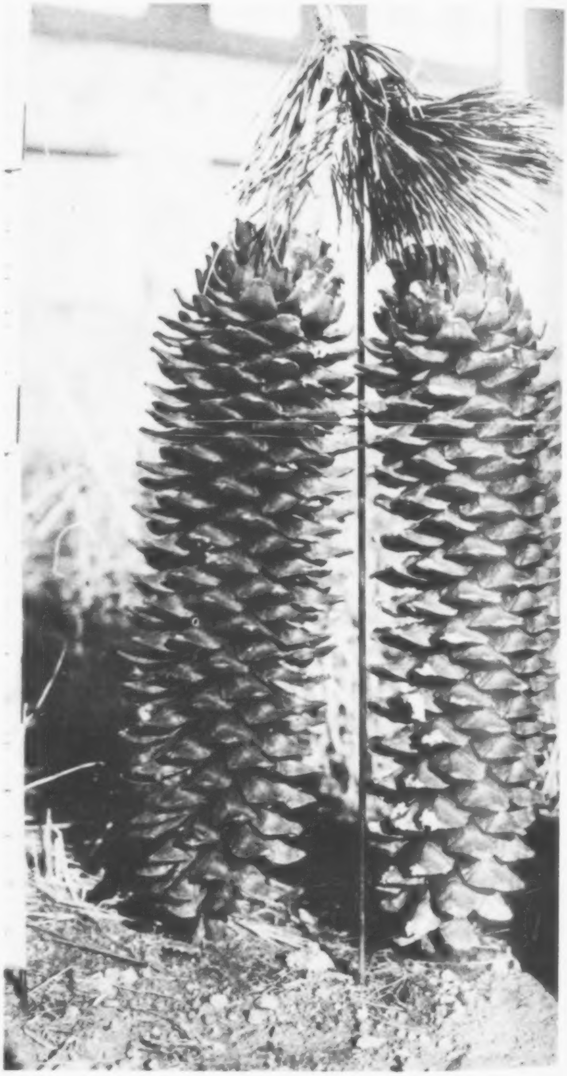

Figure 2—*Sugar pine cones.*

Cone production starts later and is less prolific in sugar pine than in its associates. During a 16-year study in the central Sierra, fewer than 5 percent of sugar pines less than 20 cm (8 in) in d.b.h., and 50 percent less than 31 cm (12 in) in d.b.h., produced cones. Of trees 51 cm (20 in) or more, 80 percent produced cones, and dominant trees produced 98 percent of the total. Intervals between heavy cone crops averaged 4 years and ranged from 2 to 7 *(12)*.

Loss of sugar pine cones is heavy; the probability of a pollinated conelet developing to maturity is only 40 to 50 percent. Predation by the sugar pine cone beetle *(Conophthorus lambertianae)* can cause up to 93 percent loss. Douglas squirrels and white-headed woodpeckers also take a heavy toll *(7,11,17)*.

Spontaneous abortion of first-year conelets is high. Observations of control-pollinated trees in the Klamath Mountains showed that 19 percent of female strobili were lost 5 to 12 weeks after bagging, with no obvious signs of insect or pathogen-caused damage *(41)*. The amount of abortion varied from 15 to 85 percent among trees, for both bagged and unbagged strobili. Since this pattern was consistent in successive years, a genetic cause was suggested.

Seed Production and Dissemination—Mature trees produce large amounts of sound seeds. In a study of 210 trees in 13 stands in the central and northern Sierra Nevada, the average number of sound seeds per cone was 150, with individual trees ranging from 34 to 257. Higher numbers of seeds per cone (209 to 219) have been reported, but whether the count was based on sound or total seeds was not specified. In good crop years, the proportion of sound seeds is usually high (67 to 99 percent) but in light crop years can fall as low as 28 percent *(7,12)*.

Cones are ripe and start to open when their color turns light brown and specific gravity (fresh weight basis) drops to about 0.62. Seed shed may begin in late August at low elevations and at higher elevations is usually complete by the end of October *(11)*.

Seeds are large and heavy, averaging 4,630 seeds per kilogram (2,100/lb). Since their wings are relatively small for their size, seeds are not often dispersed great distances by wind, and 80 percent fall within 30 m (100 ft) of the parent tree. Birds and small mammals may be an important secondary mechanism of dispersal, even though they consume most of the seeds they cache. In good seed years, large amounts of seed fall, with estimates ranging from 86,500 to more than 444,800/ha (35,000 to 180,000/acre) in central Sierra Nevada stands *(11,32)*.

Seedling Development—Sugar pine seeds show dormancy, which can be readily broken by stratification for 60 to 90 days or by removal of the seed coat and inner papery membrane surrounding the seed. Germination of fresh seed is uniformly rapid and high, exceeding 90 percent if adequately ripened, cleaned, and stratified. Viability may decline rapidly with time in storage at temperatures above freezing, but deep-frozen seed maintains viability much longer *(1,32,47)*.

On unprepared seed beds, seed-to-seedling ratios are high (244 to 483). Soil scarification reduced the ratio to 70 in one case, and scarification with rodent poisoning dropped it to 38 in another *(12)*.

Seedling losses are continual and only 20 to 25 percent of the initial germinants may survive as long as 10 years. Drought may kill up to half of the first-year seedlings. Cutworms and rodents, which eat seeds still attached to seedling cotyledons, also take their toll *(11,12)*. Seedlings infected by blister rust rarely survive more than a few years.

Germination is epigeal *(32)*. Seedlings rapidly grow a deep taproot when seeds germinate on bare mineral soil. In one comparison, taproots penetrated to an average depth of 43 cm (17 in) on a bare sandy soil, but only half as deep when the soil was overlain with duff *(11)*. Lateral roots develop near and parallel to the soil surface, often growing downward some distance from the stem. In heavier, more shallow soils, laterals are often larger than taproots. During the second season, laterals commonly originate on the lower taproot and occupy a cone of soil which has its base at the tip of the taproot. After 2 years on three different soil types in Oregon, the taproots of natural sugar pine seedlings ranged from 56 to 102 cm (22 to 40 in), were significantly deeper than those of Douglas-fir and grand fir, but shorter than those of ponderosa pine and incense-cedar. Lengths of main lateral roots showed the same species differences. Top-to-root ratios for sugar pine ranged from 0.17 to 0.28 (length) and from 1.33 to 1.60 (dry weight) *(46)*.

Seasonal shoot growth starts later and terminates earlier in sugar pine than in its usual conifer associates, except white fir. At middle elevations in the central Sierra Nevada, shoot elongation begins in late May, about 2 weeks after ponderosa pine and a month before white fir, and lasts about 7 weeks. Radial growth begins about 6 weeks earlier than shoot growth and extends throughout the summer *(11)*.

Planting of sugar pine has not been so easy or successful as for some of the yellow pines. Although reasons for the many recorded failures are often complex, lower drought tolerance may be one of the factors. During natural regeneration, the ability of sugar pine seedlings to avoid summer drought by rapidly growing a deep taproot largely compensates for the relative intolerance of tissues to moisture stress *(38)*.

To survive the first summer after planting, seedlings must have the capacity to regenerate vigorous new root systems. For other western conifers, root growth capacity is conditioned by particular combinations of nursery environment and time in cold storage after lifting; these requirements are species and seed-source specific *(22,24,38)*. Although patterns of root growth capacity have not been worked out for sugar pine, it is clear that amounts of root growth are substantially less for sugar pine than for its associates *(23)*.

Early top growth of sugar pine is not so rapid as that of western yellow pines, and 1-year stock is too small for planting when seed is sown in May, for years the tradition in California nurseries. Root diseases, to which young sugar pines are unusually vulnerable, can compound the problem by weakening seedlings that survive, thus reducing their chances of establishment on the site. Sowing stratified seed in February or March extended the growing season and produced healthy seedlings of plantable size in one season *(23)*. A more expensive alternative to bareroot stock that holds some promise is containerized seedlings grown under accelerated growth regimes *(28)*.

Vegetative Reproduction—Sugar pine does not sprout, but young trees can be rooted from cuttings. The degree of success is apparently under strong genetic control. In one trial the proportion of cuttings that rooted from different ortets from 3 to 6 years old ranged from 0 to 100 percent *(27)*. As for most conifers, rootability diminishes rapidly with age of donor tree. Grafts, however, can be made from donors of all ages, with success rates from 70 to 80 percent common. Problems of incompatibility, frequent in some species such as Douglas-fir, are rare in sugar pine.

Sapling and Pole Stages to Maturity

Growth and Yield—Veteran sugar pines (fig. 3) often reach great size. Large trees have commonly scaled 114 to 142 m^3 (20,000 to 25,000 fbm, Scribner log rule), with a record of 232 m^3 (40,710 fbm). A "champion," located on the North Fork of the Stanislaus River in California, measured 65.8 m (216 ft) tall and 310 cm (122 in) in d.b.h., but trees up to 76 m (250 ft) tall have been reported *(11,36)*. These and previous champions of this century are dwarfed by the first sugar pine measured by David Douglas and described in his diary *(37)*: "Three feet from the

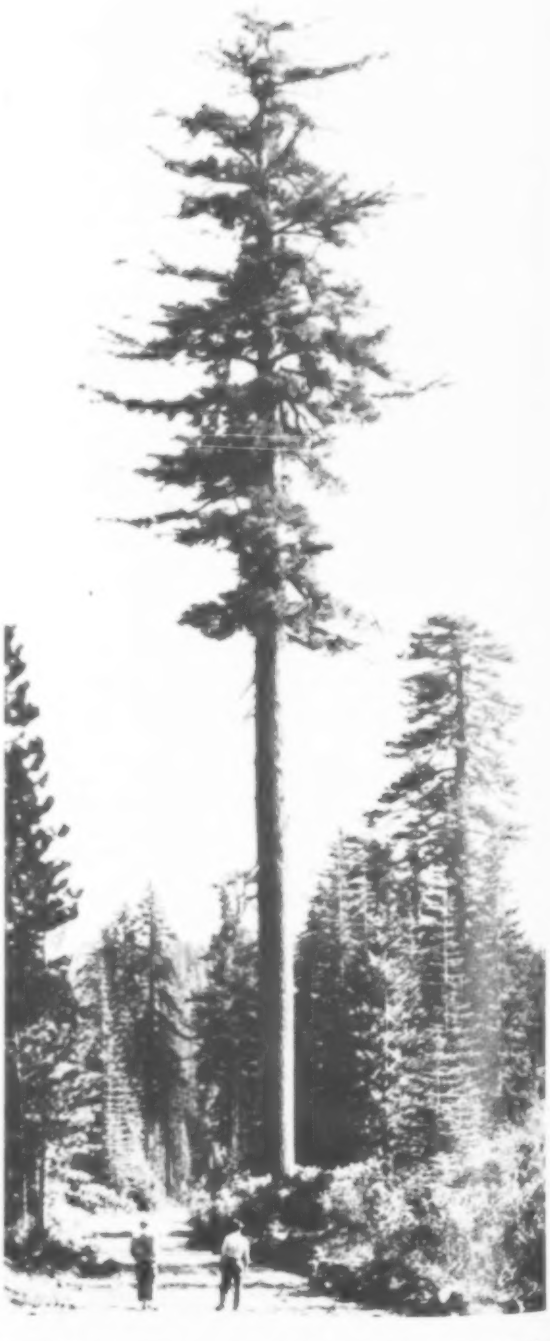

Figure 3—*Mature sugar pine. (Courtesy of Western Wood Products Assoc., Portland, OR.)*

ground, 57 feet 9 inches in circumference; 134 feet from the ground, 17 feet 5 inches; extreme length 215 feet."

Early growth of sugar pine is slow compared with ponderosa pine, but growth rates accelerate in the pole stage and are sustained for longer periods than those of common associates. Consequently, sugar pines are usually the largest trees, except for giant sequoia, in mature and old-growth stands. On better sites annual growth increments in basal area of 2.5 percent and more can be sustained up to stem diameters of 76 to 127 cm (30 to 50 in) or for 100 to 150 years *(11)*. Growth of sugar pine is best between 1370 and 1830 m (4,500 and 6,000 ft) in the central Sierra Nevada, between the American and San Joaquin Rivers.

In young mixed conifer stands, sugar pine often constitutes a relatively small proportion of the total basal area but contributes disproportionately to growth increment. On the El Dorado National Forest in the western Sierra Nevada, in stands ranging in age from 50 to 247 years, the sugar pine component was only 6 to 7 percent (range: 3 to 14 percent) of the average basal area, but its average annual basal area growth was 11.3 percent (range: 2 to 35 percent) of the stand total. A similar relationship was found on the Plumas National Forest in the northern Sierra Nevada: in stands from 58 to 95 years old, average basal area of sugar pine was 7 percent (3 to 16), but 10-year growth was more than 12 percent (6 to 19). Ten-year volume increment in mixed conifer stands from 40 to 80 years old was greater for sugar pine than for Douglas-fir, white fir, ponderosa pine, and incense-cedar in each of five basal area categories *(9)*. Mean increment for sugar pine was 4.1 percent, compared to 3.1 percent for all others.

Yields of sugar pine are difficult to predict, because it grows in mixes of varying proportion with other species. In the old-growth forest, the board foot volume of sugar pine was 40 percent of total in stands dominated by ponderosa pine and sugar pine. In exceptional cases on very small areas, yields were 2688 m^3/ha (192,000 fbm/acre) *(11)*. Yield tables for young growth are based on averages for all commercial conifers and assume full stocking *(8)*. The data base is limited, so the tables are at best a rough guide. Realistically, yields may reach 644 m^3/ha (46,000 fbm/acre) in 120 years on medium sites, and up to 1190 m^3/ha (85,000 fbm/acre) in 100 years on the best sites, with intensive management *(11)*.

Rooting Habit—Sugar pine develops a deep taproot at an early age.

Reaction to Competition—Sugar pine tolerates shade better than ponderosa pine but is slightly less tolerant than incense-cedar and Douglas-fir and much less so than white fir *(14)*. A seral species, it becomes less tolerant with age, and overtopped trees decline unless released *(11)*. Thus, dominant sugar pines in old-growth stands were probably dominant from the start, or released by natural causes early in life. White fir would usually be the climax species in mixed conifer forests in the absence of any natural disturbance; however, fire, insects, disease, and other agents are natural and pervasive features of these forests. Such disturbances frequently cause gaps, in which the relatively tolerant sugar pine is adapted to grow *(14)*. For these reasons, sugar pine is often adapted to regenerate in a shelterwood silvicultural system *(33)*.

Competition from brush severely retards seedling establishment and growth. Only 18 percent of seedlings starting under brush survived over a period of 18 to 24 years, and after 10 years the tallest seedlings measured were only 29 cm (11.4 in). Given an even start with brush, however, seedlings can compete successfully *(11)*.

Light shelterwoods can protect seedlings of sugar pine and white fir against frost, which seldom affects ponderosa and Jeffrey pines, and provide them with a competitive advantage because of their greater tolerance to shade *(13,43,44)*. On the other hand, young sugar pines stagnate beneath an overstory and in competition with root systems of established trees or brush. But because they respond well to release, the basal area increment of sugar pines is often double that of companion species after heavy thinnings *(33)*. Thus, skill in the amount and timing of overstory removal is a key factor in successful silvicultural management of sugar pine.

Sugar pine does not self-prune early, even in dense stands, and mechanical pruning is necessary to ensure clear lumber of high quality.

Damaging Agents—The pathology of sugar pine is dominated by white pine blister rust, caused by *Cronartium ribicola*, a disease serious enough to severely limit natural regeneration in areas of high hazard, and thereby alter successional trends. Among commercially important North American white pines, sugar pine is the most susceptible. Infected seedlings and young trees are inevitably killed by cankers girdling the main stem.

Blister rust was introduced into western North America shortly after the turn of the century at a single point on Vancouver Island and has since spread eastward throughout the Inland Empire and south through the Cascade, Klamath, North Coast, and Sierra Nevada Ranges. It has not yet been found in the Transverse or Peninsular Ranges of southern California, even though alternate host species are abundant there. Within the range of sugar pine, conditions for infection are not nearly so uniform as for western white pine in the Inland Empire. Incidence and intensity of infection on sugar pine are highest in Oregon and northern California and become progressively less to the south, as climate becomes warmer and drier. Within any area, however, hazard varies widely and depends on local site conditions. These are complex, but two of the most important factors are the duration of moisture retention on foliage following rain, fog, or dew, and the distribution and density of the alternate hosts, currant and gooseberry bushes *(Ribes* spp.). Thus, cool north slopes are more hazardous than warm south slopes, and relatively humid stream bottoms and lakesides are more hazardous than upland sites. In the Cascade Range and Sierra Nevada of northern California, infection averaged two to three times higher near stream bottoms than on adjacent slopes *(4)*.

Attempts to control blister rust by chemical therapy or eradicating alternate hosts have been abandoned as impractical and ineffective. Except on highly hazardous sites, sugar pine in natural stands can be effectively managed by judiciously selecting leave trees with cankers relatively far from the bole and by pruning cankers in the lower crown *(4)*.

Plantations are a much more serious problem. The microenvironmental changes on a site following clearcutting—including dew formation on foliage and the rapid regeneration of alternate host *Ribes* spp.—greatly augment the probability of rust intensification and spread on both hosts. Uniform age and stocking make sugar pine plantations vulnerable to nearly total destruction for 20 years or longer. Genetically resistant sugar pines in mixture with other conifers offer the most promising solution.

Dwarf mistletoe *(Arceuthobium californicum)* may seriously damage infected trees by reducing growth in height, diameter, and crown size, and predisposing weakened trees to attack by bark beetles. Extending throughout the range of sugar pine, except for isolated stands in Nevada, the south Coast Ranges of California, and Baja California, this mistletoe was found in only 22 percent of the stands examined and on only 10 percent of the trees in those stands. Spread is slow and can be controlled by sanitation cutting *(20,42)*.

A needle cast caused by *Lophodermella arcuata* is occasionally and locally damaging. Root diseases caused by *Armillaria mellea, Heterobasidion annosum,* and *Verticicladiella wageneri* are capable of killing trees of all ages and sizes but, though widespread, are usually at endemic levels. Several trunk and butt rots attack sugar pine but are usually confined to mature and overmature trees *(2,21)*.

Several root and damping-off pathogens cause severe damage to sugar pine in nurseries, with annual losses up to 50 percent *(45)*. In approximate order of importance, these are *Fusarium oxysporum, Macrophomina phaseoli,* and species of *Pythium, Phytophthora*, and *Rhizoctonia*. In addition to causing direct losses in the nursery, these diseases may reduce field survival of planted seedlings in more stressful environments by causing stunting and chlorosis. Nursery fumigation controls most of the organisms involved but is least effective on *Fusarium*. A simple and promising alternative control method is early sowing of stratified seed. Soil temperatures in late winter and early spring permit seed germination and root development but are still cool enough to inhibit fungal growth.

Sugar pine hosts many different insects, but the mountain pine beetle *(Dendroctonus ponderosae)* is of overwhelming importance. This insect can cause widespread mortality, often killing large groups of trees *(48)*. Several other bark-feeding insects contribute directly or indirectly to mortality in sugar pines, particularly after periods of drought. Death results from predisposing trees to mountain pine beetle. The red turpentine beetle *(Dendroctonus valens)* is usually restricted to small areas near the root crown but during drought may extend two or more meters up the bole, destroying the entire cambium. The California flatheaded borer *(Melanophila californica)* usually attacks decadent and unhealthy trees, but trees under heavy moisture stress are also vulnerable. The California fivespined ips *(Ips paraconfusus)* is only capable of penetrating thin bark in sugar pine. Small trees are often killed, but large trees only top-killed *(16)*.

The sugar pine cone beetle *(Conophthorus lambertianae)* can be extremely destructive to developing second-year cones, destroying up to 75 percent of the crop in some years. Since stunted cones are apparent by mid-June, the extent of the crop loss can be assessed well before cone collection. The sugar pine scale *(Matsucoccus paucicicatrices)* occasionally kills foliage and branches, predisposing trees to bark beetle attack. The dead "flags" resulting from heavy attack mimic advanced symptoms of white pine blister rust. Occasionally, the black pineleaf scale *(Nuculaspis californica)* defoliates sugar pine at midcrown, weakening the tree. These scale attacks are often associated with industrial air pollution or heavy dust deposits on foliage *(16)*.

Among its coniferous associates, sugar pine is the most tolerant to oxidant air pollution *(34)*, while intermediate in fire tolerance *(39)* and frost tolerance *(43,44)*. It is less tolerant of drought than most companion species with which it has been critically compared, including knobcone *(Pinus attenuata)* and Coulter pines *(50,51)*, ponderosa pine, Douglas-fir, incense-cedar, and grand fir *(40)*.

Special Uses

Upper grades of old-growth sugar pine command premium prices for specialty uses where high dimensional stability, workability, and affinity for glue are essential. The wood is light (specific gravity, 0.34 ± 0.03) *(3)*, resists shrinkage, warp, and twist, and is preferred for finely carved pattern stock for machinery and foundry casting. Uniformly soft, thin-celled spring and summer wood and straight grain account for the ease with which it cuts parallel to or across the grain, and for its satin-textured, lustrous finish when milled. Its easy working qualities favor it for molding, window and door frames, window sashes, doors, and other special products such as piano keys and organ pipes. Wood properties of young growth are not so well known. Pruning would undoubtedly be required to produce clear lumber during short rotations.

Genetics

Sugar pine is one of the more genetically variable members of the genus. Average heterozygosity of specific genes coding for seed proteins (isozymes) was 26 percent, a value near the upper range (0 to 36 percent) of pines studied so far *(6)*. How adaptive variation is distributed over the range of environments encountered in over 14° of latitude and 2000 m (6,560 ft) of elevation is largely unknown, however, because of a lack of field data from provenance or progeny tests.

In a 3-year nursery trial, pronounced differences in height and diameter growth were found among seedlings of five seed sources sampled along an elevational transect on the west slope of the Sierra Nevada *(18)*. The fastest growing seedlings were from the lower-middle elevation (1100 m or 3,595 ft) and were twice the height of those from the highest elevation (2195 m or 7,200 ft). Except for the source from the lowest elevation (770 m or 2,525 ft), which ranked second, growth varied inversely with elevation. Elevation of the seed source accounted for 52 percent of the total variance among seedlings, and the component of variance for families within stands was a substantial 16 percent. More comprehensive nursery trials, of families from seed parents ranging from southern California to southern Oregon, showed similar trends *(27)*. Greatest growth was expressed in seedlings from intermediate elevations in the central Sierra Nevada, a result consistent with observations in natural stands. Thus, genetic adaptation to climatic variables associated with elevation is clearly evident in sugar pine, requiring a close match between seed source and planting site in artificial regeneration. The degree of variability expressed among progenies of different seed parents within seed collection zones indicates that selection for rapid early growth should be effective.

Resistance to white pine blister rust is strongly inherited, and three different kinds have been recognized *(29)*. A rapid, hypersensitive reaction to invading mycelium is conditioned by a dominant gene. This gene, which occurs at variable but relatively low frequencies throughout the range of sugar pine, is highly effective against most sources of inoculum. A race of blister rust capable of overcoming this gene was discovered in a plantation in the Klamath Mountains *(30)*, but evidently had not spread from this site 10 years after it was found *(31)*. In certain families, another kind of resistance is expressed by slower rates of infection and mortality, fewer infections per tree, and by a higher rate of abortion of incipient infections. This "slow rusting" is apparently inherited quantitatively and, while less dramatic than single gene resistance, may be more stable to variation in the pathogen in the long term. Probably two or more generations of selection and breeding will be necessary to accumulate enough genes in parental stock to make this kind of resistance usable in commercial silviculture. A third kind of resistance is age-dependent. In common garden tests, infection among grafted clones from mature trees ranged from 0 to 100 percent, yet offspring from the apparently resistant clones were fully susceptible. Although not understood, the mechanisms and inheritance of mature tree resistance are very strong and could play a significant role in stabilizing resistance over a rotation. Since all three kinds of resistance are inherited independently, there is a real promise for an enduring and well-buffered genetic control of this most destructive disease.

Hybrids

Barriers to crossing with other white pines are very strong in sugar pine *(7)*. No natural hybrids are known and repeated attempts to cross sugar pine with other North American white pines have failed. Small numbers of F_1 hybrids were made with two Asiatic white pines, however: Korean pine *(Pinus koraiensis)* and Armand pine *(P. armandii)*. These

best copy available

species are of silvicultural interest because of their relative resistance to blister rust. Mass production of F_1 seed is probably impractical because of low seed set, but backcrosses of *P. lambertiana* × *armandii* to sugar pine have yielded abundant sound seed. In limited field tests, the backcross progenies were more resistant than intraspecific crosses of the same sugar pine parents. By using a broader genetic base of *P. armandii*, resistance in the backcross could be improved.

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Pinus monophylla Torr. & Frem. Singleleaf Pinyon

Pinaceae Pine family

R. O. Meeuwig, J. D. Budy, and R. L. Everett

Singleleaf pinyon *(Pinus monophylla)*, also called pinyon, nut pine, one-leaf pine, and piñon (Spanish), is a slow-growing, low, spreading tree that grows on dry, low mountain slopes of the Great Basin. One large tree near Reno, NV, is about 112 cm (44.2 in) in d.b.h., 16.2 m (53 ft) tall, and has a crown spread of about 20 m (66 ft). Principal uses of the tree include fuel, fenceposts, Christmas trees, and edible seeds.

Habitat

Native Range

Singleleaf pinyon (fig. 1) is the predominant tree species in the Great Basin. It dominates extensive areas in the dry mountain ranges of Nevada, southern and eastern California, and western Utah. Some stands are in Baja California, northwestern Arizona, and southeastern Idaho.

Climate

Singleleaf pinyon grows under more xeric conditions than any other pine in the United States. Its climate is similar to that of pinyon *(Pinus edulis)*, but during the growing season, relative humidity and precipitation are even lower and potential evapotranspiration is greater.

Average annual precipitation ranges from about 200 mm (8 in) to about 460 mm (18 in) but precipitation varies widely from year to year. Most of the precipitation occurs during the winter months (December to April), usually as snow. Mean annual temperature is about 10° C (50° F). The mean maximum temperature in July, the hottest month, is about 30° C (86° F). The mean minimum temperature in January, the coldest month, is about –6° C (21° F).

Tree growth usually starts in April and usually ceases in September or October. During most of this time, the trees depend on soil moisture stored by winter precipitation.

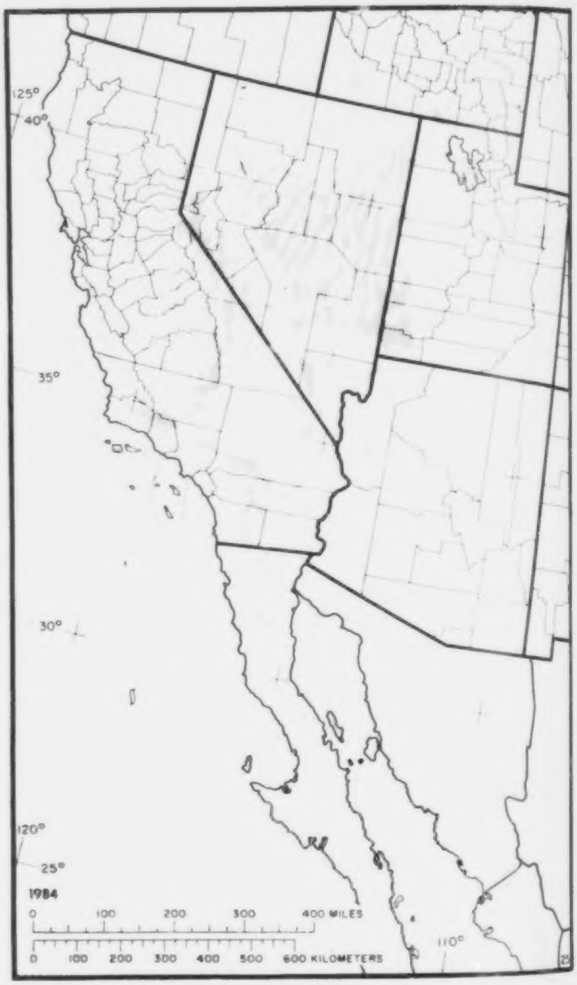

Figure 1—*The native range of singleleaf pinyon.*

Soils and Topography

Singleleaf pinyon grows on pediments, slopes, and ridges. It grows best on coarse textured, well drained Mollisols and is rarely found on valley floors. Soils are both residual and alluvial and are derived from granite, rhyolite, andesite, limestone, and a variety of other parent materials. Soil depth and age are highly variable. Surface soil pH usually is between 6.0 and 8.0. Trees impact soils by changing soil

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nutrient distribution both laterally and vertically in the soil profile and concentrating nutrients under the crowns *(5)*.

The elevational range of singleleaf pinyon is usually between 1000 m (3,280 ft) and 2800 m (9,200 ft), depending on local conditions. In the high desert of the Great Basin, the lower limit is somewhat above the elevation of the adjacent valleys, varying from about 1520 m to 2130 m (5,000 to 7,000 ft). In Baja California and parts of California, singleleaf pinyon can be found below 1000 m (3,280 ft) *(9)*. The upper elevational limit varies with local climate and presence of competing tree species. Singleleaf pinyon has been reported at 3050 m (10,000 ft) in the White Mountains of California *(21)*.

Associated Forest Cover

Throughout its range, singleleaf pinyon is the major component of the forest cover type Pinyon-Juniper (Society of American Foresters Type 239) *(6)*. Utah juniper *(Juniperus osteosperma)* is present in varying amounts in most singleleaf pinyon stands. Pinyon is usually the dominant species, but juniper tends to be dominant along the northern geographical limit of pinyon and near the lower elevational limit of pinyon in many areas. Utah juniper is absent from some pinyon stands in western and southern Nevada and from most pinyon stands in southern California. California juniper *(J. californica)* replaces Utah juniper in some southern California pinyon woodlands *(9)*.

Curlleaf mountain-mahogany *(Cercocarpus ledifolius)* is associated with singleleaf pinyon in many areas, particularly near the upper elevational limit of pinyon. In the Sierra Nevada, singleleaf pinyon can be found growing with Jeffrey pine *(Pinus jeffreyi)*, ponderosa pine *(P. ponderosa)*, and western juniper *(Juniperus occidentalis)*. Singleleaf pinyon has been found growing with bristlecone pine *(Pinus aristata* var. *longaeva)* in the White Mountains of California *(21)*, on several mountain ranges in Nevada, and in the San Francisco Mountains of southwestern Utah *(14)*.

There is a great diversity of undergrowth vegetation associated with singleleaf pinyon woodlands, and coverages vary with site quality and successional stage. Early successional stages following fire or tree harvesting are often dominated by several weedy annuals: coyote tobacco *(Nicotiana attenuata)*, ground smoke *(Gayophytum ramosissimum)*, stickseed *(Lappula redowskii)* and root sprouting shrubs: rabbitbrush *(Chrysothamnus* spp.), ephedra *(Ephedra* spp.), snowberry *(Symphoricarpos* spp.), and desert peach *(Prunus andersonii) (3)*. The invasion of Cheatgrass *(Bromus tectorum)* on disturbed pinyon sites can create a fire disclimax community that inhibits shrub and subsequent tree establishment. Other shrubs that often establish from soil seed reserves or immigrate rapidly to disturbed sites include mountain big sagebrush *(Artemisia tridentata* var. *vaseyana)*, basin big sagebrush *(A. tridentata* var. *tridentata)*, Wyoming big sagebrush *(A. tridentata* var. *wyomingensis)*, low sagebrush *(A. arbuscula)* (fig. 2), black sagebrush *(A. nova)*, sulfur eriogonum *(Eriogonum umbellatum)*, and antelope bitterbrush *(Purshia tridentata)*. Associated grasses include Sandberg blue grass *(Poa sandbergii)*, bottlebrush squirreltail *(Sitanion hystrix)*, Nevada bluegrass *(Poa nevadensis)*, Idaho fescue *(Festuca idahoensis)*, bearded bluebunch wheatgrass *(Agropyron spicatum)*, Great Basin wildrye *(Elymus cinereus)*, and needle-and-thread grass *(Stipa comata) (24)*. All perennial understory species decline during stand development.

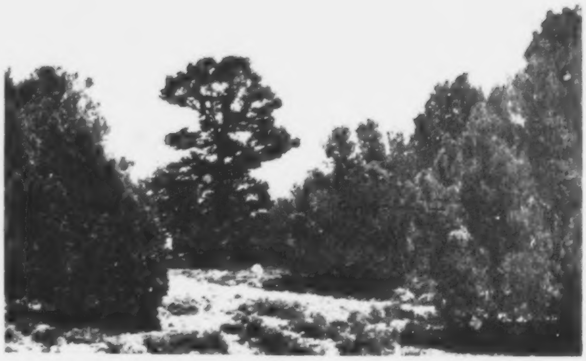

Figure 2—*A singleleaf pinyon—low sagebrush* (Artemesia arbuscula) *community in Mono County, CA.*

Life History

Reproduction and Early Growth

Flowering and Fruiting—Singleleaf pinyon is monoecious and requires two seasons between flowering and seed ripening. Male and female strobili emerge from buds in late spring or early summer. The staminate cones usually begin to shed pollen by mid-June when the young ovulate cones are receptive to pollination. Growth and development of the cones are slow during the first growing season. By September the cones are about one-fourth their mature length. Fertilization occurs the following spring, about 1 year after pollination. The cones grow rapidly during the second growing season. Three to four cones may mature on each branchlet. As the cones mature in early September they turn from green to brown. Cone-opening may last from September to early November depending on environmental conditions and elevation.

Mature cones range in length from 3.7 to 8.3 cm (1.5 to 3.3 in) and average 5.5 cm (2.2 in). The number of sound seeds per cone varies from 2 to 60 with an average of 20. The number of seeds per kilogram ranges from 1,200 to 3,400 (540 to 1,540 seeds/lb), with an average of 2,000 seeds per kilogram (900/lb). The viability of fresh seeds is high, but shelf life is short. The germination of some seed lots decreased from 90 percent before storage to 10 percent after 6 months of cold storage. Because the average moisture content of freshly collected seeds is 30 percent (wet weight basis), seeds should be dried before storing.

Seed Production and Dissemination—Seed production by singleleaf pinyon is highly variable. It varies from tree to tree, from year to year, and from place to place. The interval between good seed crops in any particular area varies from 3 to 7 years, yet good seed crops occur somewhere in the Great Basin woodlands nearly every year. Generally, singleleaf pinyon trees do not begin bearing cones before they are 35 years old and do not begin producing good seed crops earlier than 100 years. A productive tree yields about 5 kg (11 lb) of seeds in a good year, but some trees never yield good crops.

The heavy wingless seeds are not adapted to wind dispersal but tend to fall to the duff under the parent tree. The seeds are disseminated locally by rodents and over distances by birds. These animals consume most of the seed but leave some to germinate in place or in caches, especially when seed production is above average.

Seedling Development—Pinyon depends upon a standing crop of seedlings for species perpetuation. Seedlings require a nurse crop; thus, most seedlings are found under shrubs in mid succession and under the tree crown in late succession *(4)*. Germination is epigeal. Although pinyon seedlings germinate in the open, few survive without some degree of protection from direct solar radiation. Top growth during the seedling stage is extremely slow. Seedling height growth usually is less than 2.5 cm (1.0 in) per year and diameter growth usually is less than 0.3 mm (0.012 in) per year. Root growth, however, is quite rapid. The thick taproot can reach 15 cm (6 in) in 10 days after germination. Seedlings growing under low shrubs usually have greater diameter growth and less height growth than those under tree canopies. Seedlings maintain a more favorable water status and have greater drought avoidance than the shrub nurse plant *(2)*. This phenomena facilitates seedling survival and tree encroachment into adjacent shrub communites.

Vegetative Reproduction—Singleleaf pinyon does not reproduce naturally by vegetative means.

Sapling and Pole Stages to Maturity

Growth and Yield—Singleleaf pinyon is one of the slowest growing conifers. It usually requires about 60 years to attain a height of 2 m (6.6 ft). Average annual height growth of immature dominants is about 5 cm (2 in). Height growth rates vary considerably among individual trees, even among those on identical sites. Heights of mature dominants range from about 6 m to 12 m (20 to 40 ft), depending on site quality and genotype *(17)*. One pinyon 14 m (46 ft) tall has been reported *(19)*.

Because singleleaf pinyon tends to have large branches or multiple stems at breast height, diameter and basal area measurements are taken more conveniently near ground level, usually at 15 cm (6 in) above the ground (stump height). Diameter growth rates are greatly influenced by competition for severely limited water supplies. Average annual diameter growth of dominant trees is 1 to 5 mm (0.04 to 0.20 in). The average dominant tree takes about 150 years to reach a stump height diameter of 30 cm (12 in). There is no definite age of culmination of diameter growth; pinyon trees in strongly dominant positions can maintain essentially constant diameter growth rates for more than 200 years. Reductions in diameter growth rates are caused by increasing competition as stands develop, rather than by tree age *(17)*.

Average annual basal area growth of fully stocked stands is about 0.25 m^2/ha (1.1 ft^2/acre) on typical sites, as low as 0.09 m^2/ha (0.4 ft^2/acre) on poor sites, and as high as 0.55 m^2/ha (2.4 ft^2/acre) on good sites. Average annual aboveground biomass accumulation rates of fully stocked stands varies from about 0.2 to about 2.2 t/ha (0.1 to 1.0 ton/acre), depending on site quality. On average sites it is about 0.9 t/ha (0.4 ton/acre) *(17)*. Total aboveground biomass averages 150 t/ha (67 ton/acre) of which 60 percent is in the tree and 40 percent is in the forest floor.

Singleleaf pinyon trees more than 300 years old are fairly common on poor sites but rare on good sites. It appears that all the better sites were either burned in the past 300 years or have been cut over in the past century or so. The poorer sites are virtually fireproof because their sparse vegetation will not carry fire, and these sites were not cut because of the small size and poor form of their trees. The maximum lifespan of singleleaf pinyon is probably greater than 600 years. A healthy tree 433 years old and 100 cm (40 in) diameter at stump height was found in the Sweetwater Mountains in east-central California *(18)*. Trees slightly older than 600 years have been reported in the Toiyabe Range in central Nevada and in the Egan Range in eastern Nevada.

Rooting Habit—Little information is available on the rooting habit of pinyon. A few excavated trees indicate root systems are comprised of a short, stunted taproot, a fibrous "feeder" root system under the tree crown, and an extensive lateral root system that extends for at least three times tree height in all directions. Complete crown closure is rare in most stands, but where the stands are well developed the soils are usually completely occupied by tree roots resulting in suppression of the understory vegetation.

Reaction to Competition—Although pinyon is intolerant of shade, water rather than light is usually the limiting factor in survival and growth. The competition for available soil moisture among trees is so intense that younger trees are usually suppressed and some eventually die. Although older trees usually survive, growth rates are greatly reduced. Suppressed trees may resume normal growth rates when released from severe moisture stress *(17)*. Light competition does not appear to be a factor because overstory foliage is rarely dense enough to reduce light intensities below tolerance levels.

Damaging Agents—Susceptibility to fire depends on the stage of development of the pinyon stand. In young stands, enough shrubby and herbaceous vegetation often exists to carry fire over extensive areas. As the stand develops, understory vegetation becomes too sparse to carry fire, and the trees generally are too widely spaced to carry a crown fire except with the aid of extremely high winds *(1)*. Thus, fire is ordinarily confined to younger stands and to a few individual lightning-struck trees in older stands.

Pinyon ips *(Ips confusus)* is endemic over the range of singleleaf pinyon. It occasionally attacks and kills trees weakened by other agents but usually causes little damage *(8)*. Minor epidemics can occur in areas where uprooted trees or slash accumulation permit the population to build up and successfully attack healthy trees. Mountain pine beetle *(Dendroctonus ponderosae)* attacks singleleaf pinyon on rare occasions.

Pinyon needle scale *(Matsucoccus acalyptus)* weakens trees by repeated feeding, which makes them more vulnerable to attack by *Ips confusus* and may kill small trees directly. The pinyon sawfly *(Neodiprion edulicolus)*, a defoliator, reduces tree vigor and renders small trees unfit as Christmas trees *(15)*. Pinyon foliage also is attacked by a number of less damaging insects including an aphid *(Pineus coloradensis)*, a beetle *(Glyptoscelis aridis)*, a scale *(Matsucoccus monophyllae)*, a stinkbug *(Dendrocoris pini)*, and a sawfly *(Zadiprion rohweri)* *(8)*.

Singleleaf pinyon nut production is sporadic, varying considerably from place to place and from year to year. Weather variations are partially responsible, but cone insects probably reduce nut production substantially. The most damaging cone insects are two moth species *(Eucosma bobana* and *Dioryctria albovittella)* and the singleleaf pinyon cone beetle *(Conophthorus monophyllae)* *(7,11)*.

Although singleleaf pinyon is attacked by a number of diseases, only three are known to cause serious injury. Pinyon dwarf mistletoe *(Arceuthobium divaricatum)* is a widespread parasite found on both singleleaf and Colorado pinyon; it causes extensive damage *(10)*. It rarely kills trees directly but renders them more susceptible to insect attack.

Pinyon blister rust *(Cronartium occidentale)* occurs extensively on *Ribes* spp. in most western states but attacks singleleaf and Colorado pinyon only in localized areas *(22)*. It occasionally kills small trees but rarely becomes epidemic.

A root disease *(Verticicladiella wageneri)* kills singleleaf pinyon in a few localized areas, notably in the San Bernardino Mountains of California *(20,25)*. It spreads by root contact and is confined to the xylem in the roots and lower trunk.

Special Uses

Because of its small size and lack of self-pruning, singleleaf pinyon is not suitable for lumber, but it is used extensively for firewood. Because most singleleaf pinyon aboveground biomass and nutrient capital is in the slash (less than 7.6 cm, 3 in, in dia.) nutrient loss from fuelwood removal is not a significant nutrient drain on the site *(23)*. Pinyon makes a desirable Christmas tree because of its fragrance and strong branches. Pinyon nuts were a staple in the diet of the Indians before white settlement and are still harvested extensively.

At present, the greatest values of the pinyon–juniper woodlands are the shelter and forage they provide numerous species of wildlife. As the demand for energy increases, the highest use will shift toward fuel production.

Genetics

The wide geographic and elevational ranges of singleleaf pinyon suggest a great deal of genetic variation. Difference in growth form, foliage color, and cone production among trees growing on identical sites are commonly observed. Little research has been done, however, on the genetics of intraspecific variation of singleleaf pinyon. Singleleaf pinyon hybridizes with Colorado pinyon *(Pinus edulis)* in Utah and Arizona where the ranges of the two species overlap *(12)*, and with Parry pinyon *(P. quadrifolia)* in southern California and Baja California *(13)*.

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Pinus monticola Dougl. ex D. Don   Western White Pine

Pinaceae   Pine family

Russell T. Graham

Western white pine *(Pinus monticola)*, also called mountain white pine, Idaho white pine, or silver pine, is an important timber tree. Its lightweight, nonresinous, straight-grained wood exhibits dimensional stability that makes it particularly valuable for sash, frames, and doors, interior paneling, building construction, match wood, and toothpicks. Western white pine grows rapidly to a large size; one of the largest standing trees measures 200 cm (78.6 in) in d.b.h. and 72.8 m (239 ft) tall in the mountains near Medford, OR.

Habitat

Native Range

Western white pine (fig. 1) grows along the west coast from latitude 35° 51′ N. in southern Tulare County, CA, to latitude 51° 30′ N. near Butte Inlet in southern British Columbia. Along the west coast, the species grows on Vancouver Island, in adjacent British Columbia, southward through Washington and Oregon, and in the Cascade Mountains *(7)*. It is also found in the Siskiyou Mountains of southern Oregon and northern California, in the Sierra Nevada of California, and near Lake Tahoe, NV.

In the interior, western white pine grows from latitude 52° 30′ N. near Quesnel Lake, BC, southward through the Selkirk Mountains of eastern Washington and northern Idaho, and into the Bitterroot Mountains in western Montana. Its southernmost interior limit is in the Blue Mountains of northeastern Oregon (latitude 44° 14′ N.). Isolated populations are found as far east as Glacier National Park, MT. It attains its greatest size and reaches its best stand and commercial development in the Inland Empire, which includes northern Idaho and adjacent sections of Montana, Washington, and British Columbia *(28)*.

Climate

The portions of Vancouver Island, the Cascade Mountains, and the Siskiyou Mountains that are within the range of western white pine have cool maritime climates, with wet winters and dry summers. Precipitation varies considerably throughout the region depending on elevation and exposure. Variation with latitude from northern Oregon through British Columbia is small, however *(25)*. In general, precipitation on Vancouver Island and in the Cascade Mountains averages from 1500 to 2010 mm (59 to 79 in) per year while precipitation in the Siskiyou Mountains averages from 510 to 1520 mm (20 to 60 in) per year. The winter snow line varies with latitude and averages 600 m (2,000 ft) elevation, with dense heavy snowpacks common. Occasionally, vegetation and the forest floor are coated with a layer of ice from glaze storms. Temperatures of the Vancouver Island–Cascade Mountain portions of the western white pine range vary from a low of -18° C (0° F) to a maximum of 38° C (100° F). January is usually the coldest month in the region and July and August are the warmest. Frost-free days range from 200 days in coastal areas to 90 days in the Cascades.

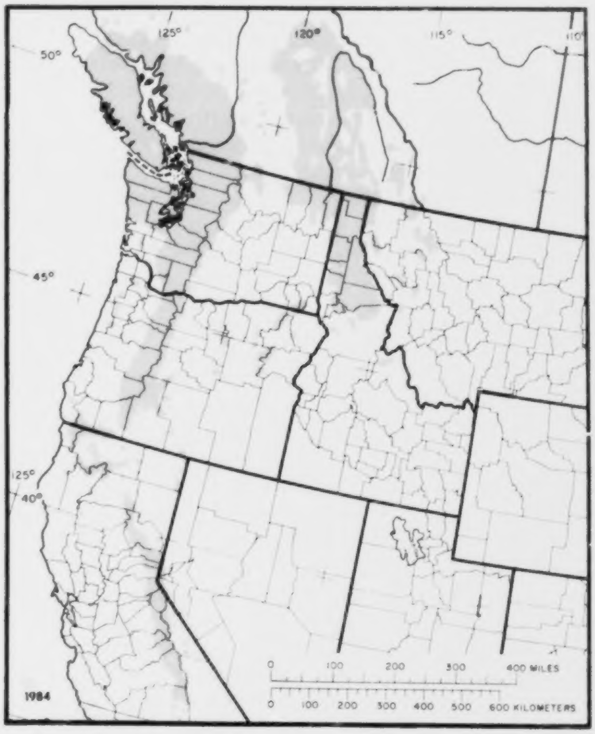

Figure 1—*The native range of western white pine.*

In the Sierra Nevada where western white pine grows, the mean annual precipitation varies from

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760 to 1500 mm (30 to 59 in). Except for occasional summer thunderstorms, this total falls entirely as snow. The temperature of the area averages between -9° C (15° F) in February to 27° C (80° F) in July and August, with maximum temperature near 37° C (98° F) and a minimum temperature near -32° C (-26° F). In the Sierra Nevada, frost-free days of the western white pine range average between 90 and 180 days, but killing frosts can occur at any time.

The climate of the Inland Empire in the western white pine range is influenced by the Pacific Ocean some 400 km (248 mi) to the west. The summers are dry, the majority of the precipitation occurring during the fall and winter. Precipitation averages between 710 and 1520 mm (28 and 60 in), distributed seasonally as follows: 35 percent, winter; 24 percent, spring; 14 percent, summer; and 27 percent, fall *(28)*. Snowfall averages 262 cm (103 in) but ranges from 122 cm (48 in) to 620 cm (244 in). Annual temperatures in the inland range of western white pine average from 4° to 10° C (40° to 50° F) with extremes of -40° and 42° C (-40° and 107° F). The growing season for western white pine in the Inland Empire is irregular depending on location and year but averages between 60 and 160 days *(28)*.

The boundaries of the western white pine range in the Inland Empire are limited at the lower elevations by deficient moisture and at the upper elevations by cold temperatures. The southern boundary of the type in the Inland Empire is not fixed by insufficient precipitation alone, but by a balance of precipitation and evaporation *(28)*.

Soils and Topography

A wide variety of soils support western white pine along the west coast of Washington and Oregon *(11)*. The species reaches its best development on deep, porous soils but is most common on poor, sandy soils. The soils are derived from a wide variety of parent material but are generally moderately deep with medium acidity. Organic matter content is usually moderate, and textures range from sandy loam to clay loam. The majority of the soils in which western white pine grows have been classified as Spodosols. In the Puget Sound area, extensive stands of western white pine grow on soils originating from glacial drift.

Soils of the Inland Empire western white pine region are very diverse. Soil depths range from 25 cm (10 in) to over 230 cm (90 in) and have developed from decomposed granite, schist, quartzite, argillite, sandstone, and shale. Most often, the more rocky soils have developed from basalt, glacial deposits, alluvial deposits, or lacustrine deposits *(28)*. In the Inland Empire, the upper soil layers that support western white pine are composed of loess or loessial-like material. As along the west coast, most of the soils that support western white pine in the Inland Empire are Spodosols.

The pH of soils supporting western white pine in the Inland Empire ranges from 4.5 to 6.8 with a mean near 5.4 *(6)*. The cation exchange capacity of these soils ranges from 20.5 to 28.5 meq/100 g with a mean of 25.1 meq/100 g. Mean concentrations of potassium, calcium, and magnesium are 0.5, 10.5, and 0.8 meq/100 g, respectively. Nitrogen content of soils of the Inland Empire western white pine range varies from 0.14 percent to 0.48 percent with a mean of 0.25 percent.

Western white pine grows at a wide range of elevations. In interior British Columbia, it grows at elevations up to 450 m (1,480 ft), while on Vancouver Island it is normally found at elevations up to 1200 m (3,940 ft) and has been found at elevations over 1500 m (4,920 ft). In western Washington, western white pine is found growing at sea level (near Puget Sound) and up to 910 m (2,980 ft) in elevation in the Cascades. Farther south in the western Cascades, it grows between elevations of 600 and 1850 m (1,970 and 6,070 ft). On the eastern side of the Cascades, it is found growing between elevations of 350 and 1450 m (1,150 and 4,760 ft). In the Olympic Mountains, the species ranges from sea level to an elevation of 550 m (1,800 ft). In the Siskiyou Mountains, western white pine is found at elevations from 1830 to 2140 m (6,000 to 7,020 ft). Farther south in the Sierra Nevada, it usually grows at elevations from 1830 to 2300 m (6,000 to 7,550 ft) with occasional trees at elevations of 3350 m (10,990 ft).

In northern Idaho and contiguous parts of Washington, Montana, and British Columbia, western white pine usually grows between 500 m (1,640 ft) and 1800 m (5,910 ft). Here the topography is usually steep and broken with V-shaped and round-bottomed valleys. Western white pine can grow on a variety of slopes and aspects but is most common along moist creek bottoms, lower benches, and northerly slopes. The most extensive bodies of western white pine are found in the wide river bottoms, less steep lower slopes, and in the more gently rolling country of the Priest, Coeur d'Alene, St. Joe, and Clearwater River basins *(28)*.

Associated Forest Cover

Western white pine is represented in 18 forest cover types of western North America and Canada. It is the key species in Western White Pine (Society of American Foresters Type 215) *(9)*. In this type western white pine constitutes a plurality of stocking, but many other species such as grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), California red fir (*A. magnifica*), lodgepole pine (*Pinus contorta*), ponderosa pine (*P. ponderosa*), western larch (*Larix occidentalis*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) may also be present. Most often the western white pine component of Type 215 is even aged with an understory containing multiaged trees of the more shade-tolerant species such as western hemlock and western redcedar. Occasionally, light overstory components of more intolerant species, such as western larch and lodgepole pine, may also be present.

In the 17 other cover types, western white pine is a common component, along with many other species, including Pacific silver fir (*Abies amabilis*), white fir (*A. concolor*), noble fir (*A. procera*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), incense-cedar (*Libocedrus decurrens*), Sitka spruce (*Picea sitchensis*), whitebark pine (*Pinus albicaulis*), foxtail pine (*P. balfouriana*), limber pine (*P. flexilis*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyi*), Pacific yew (*Taxus brevifolia*), Pacific madrone (*Arbutus menziesii*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), quaking-aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). These cover types are as follows:

205	Mountain Hemlock
206	Engelmann Spruce–Subalpine Fir
207	Red Fir
210	Interior Douglas-Fir
212	Western Larch
213	Grand Fir
218	Lodgepole Pine
224	Western Hemlock
226	Coastal True Fir–Hemlock
227	Western Redcedar–Western Hemlock
228	Western Redcedar
229	Pacific Douglas-Fir
230	Douglas-Fir–Western Hemlock
231	Port-Orford-Cedar
237	Interior Ponderosa Pine
247	Jeffrey Pine
256	California Mixed Subalpine

In northern Idaho and eastern Washington, the most important habitat types in which western white pine grows are *Tsuga heterophylla*/*Clintonia uniflora*, *Thuja plicata*/*Clintonia uniflora*, and *Abies grandis*/*Clintonia uniflora* *(6)*. Western white pine is a major seral species in the *Tsuga heterophylla*/*Clintonia uniflora* habitat type in western Montana and is also present in several others *(21)*. Western white pine is present in several vegetative associations, communities, and zones in western Oregon and Washington but is a major constituent only of the *Tsuga heterophylla* zone in the Puget Sound area of Washington *(5,11,14)*.

Most of the habitat types, associations, and communities in Washington, Oregon, and the Inland Empire where western white pine grows are strikingly rich in other woody and herbaceous flora *(5,6,11,14,21)*. In contrast, in the Sierra Nevada the vegetation associated with western white pine is characteristically sparse. Shrubs associated with western white pine include huckleberry (*Vaccinium* spp.), willow (*Salix* spp.), honeysuckle (*Lonicera* spp.), wintergreen (*Gaultheria* spp.), azalea (*Rhododendron* spp.), prickly currant (*Ribes lacustre*), sticky currant (*R. viscosissimum*), Rocky Mountain maple (*Acer glabrum*), Greenes mountain-ash (*Sorbus scopulina*), princes-pine (*Chimaphila umbellata*), snowberry (*Symphoricarpos albus*), whipplea (*Whipplea modesta*), ocean-spray (*Holodiscus discolor*), serviceberry (*Amelanchier alnifolia*), ninebark (*Physocarpus malvaceus*), rustyleaf menziesia (*Menziesia ferruginea*), spirea (*Spiraea betulifolia*), pachistima (*Pachistima myrsinites*), and twinflower (*Linnaea borealis*). Graminoids frequently associated with western white pine include sedge (*Carex* spp.), woodrush (*Luzula* spp.), Columbia brome (*Bromus vulgaris*), pine grass (*Calamagrostis rubescens*), and nodding trisetum (*Trisetum cernuum*). Forbs found growing with western white pine include false solomons-seal (*Smilacina* spp.), twistedstalk (*Streptopus* spp.), coolwort (*Tiarella* spp.), violet (*Viola* spp.), wild ginger (*Asarum caudatum*), queenscup (*Clintonia uniflora*), western goldthread (*Coptis occidentalis*), bunchberry (*Cornus canadensis*), sweetscented bedstraw (*Galium triflorum*), white trillium (*Trillium ovatum*), and Brewers lupine (*Lupinus breweri*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Western white pine is monoecious. Three complete growing seasons are required for seed to mature. Strobilus buds are differentiated during July and August of the growing season before their appearance in June the following spring *(28)*. In northern Idaho, the oval staminate strobili are about 10 cm (4 in) long, borne in clusters of 15 to 25 on branches of the middle crown, and are distinguishable about June 1 *(28)*; whereas, in the Sierra Nevada of California, the staminate strobili appear near the first of July. Pollen dissemination in the Inland Empire usually begins during the last week of June and can continue to the middle of July but usually averages 8.5 days.

The greenish-yellow to bright pink ovulate strobili are borne on stalks at tips of the upper branches, and in the Inland Empire become visible about mid-June of the growing season following initiation of the primordia. The erect conelets are from 1.5 cm to 4.0 cm (0.6 to 1.6 in) long at time of pollen dissemination, and they grow to 2.5 cm to 5.0 cm (1.0 to 2.0 in) long by the end of the first growing season *(28)*.

Time of anthesis may vary over a period of 20 days and is rigidly controlled by temperatures during the weeks immediately preceding anthesis. Anthesis is delayed about 5 days per 300 m (980 ft) increase in elevation, and about 6 days per degree Fahrenheit below normal temperatures for May and June *(28)*. In the Inland Empire, good strobilus crops in western white pine occur every 3 to 4 years, the major cycle being 4 years. Warm, dry "stress" periods, during the early summer of the 2 years before strobilus emergence, favor strobilus production. In contrast, stresses in the late summer of the year prior to emergence or during the period of emergence depress strobilus production. Within individual trees and within localities, maxima pollen shedding and ovulate anthesis practically coincide. No phenological barriers to either selfing or crossing appear to exist, but most western white pine show a moderate to strong discrimination against self-pollination. Western white pine seedlings that result from self-pollination are typically slower growing than seedlings resulting from cross-pollination *(3)*.

Western white pine is predominantly female from first strobilus production at age 7 through age 20 *(3)*. Cultural treatments, such as watering, fertilizing, and cultivating, usually have little effect on this characteristic, but thinning and fertilizing 40-year-old western white pine with nitrogen, phosphorus, and potassium has increased it *(1)*.

Seed Production and Dissemination—Cones of western white pine (fig. 2) become ripe during August and September of the second year after the strobilus buds are initiated. Color of ripe cones ranges from yellowish or beige-brown through reddish brown and dark brown *(17)*. Western white pine cones are about 20 cm to 25 cm (7.9 to 9.8 in) long; cones as short as 5 cm (2.0 in) and as long as 36 cm (14.2 in) have been reported. Over 18 years, 380 western white pine from 25 to 70 years old in the Inland Empire produced from 2 seeds to more than 300 seeds per cone, with a mean production of 226 *(2)*.

Figure 2—*Western white pine with a good cone crop in the Wenatchee National Forest, WA.*

Western white pines can begin cone production as early as age 7 and become more prolific with age. Not until trees are about age 70 does cone production become both frequent and abundant. It continues to increase with age until trees are about 50 cm (19.7 in) in diameter. After that, seed production depends on individual tree vigor and character of crown or possibly on heritable capacity to set and bear cones *(28)*.

Seed yields for western white pine range from 30,900 to 70,500/kg (14,000 to 32,000/lb) with an average of 59,000/kg (27,000/lb) *(17)*. In the Inland Empire, seed production varies from 41,000 to 457,000/ha (16,600 to 185,000/acre), with average annual seed yields for a 75-year-old stand and an overmature stand of 8,600/ha (3,500/acre) and 99,000/ha (40,100/acre), respectively.

Several cone and seed insects and rodents can cause partial to almost complete failures of cone crops in otherwise poor to fair crop years. The cone beetles, *Conophthorus monticolae* and *C. lambertianae*, and cone moths, *Dioryctria abietivorella* and *Eucosma rescissoriana*, cause serious seed losses some years *(12)*. Western white pine seeds are also a favorite food of red squirrels and the deer mouse.

In the Inland Empire, seed dissemination of western white pine begins in early fall; 15 percent of the current crop reaches the ground before September 1, about 85 percent by the end of October, and 15 percent during the late fall and winter *(28)*. Seeds are usually disseminated by wind, but squirrels, mice, and various birds contribute to seed dissemination. Most seeds fail within 120 m (390 ft) of the parent tree, but they have been known to travel over 800 m (2,620 ft) from it *(28)*.

Western white pine seeds remain viable after overwinter storage in duff on the forest floor. Seeds have shown 40 percent viability after one winter's storage, and 25 percent viability after two winters' storage; and less than 1 percent after 3 and 4 years' storage. Western white pine seeds properly stored under artificial conditions of seed moisture content of 5 to 10 percent and temperatures of -18° C (0° F) to -15° C (5° F) remain viable for 20 years *(17)*.

Seedling Development—Western white pine seed requires 30 to 120 days of cold, moist conditions before germination commences *(17)*. Seed dormancy appears to be controlled by the seed coat, papery seed membrane, and physiological elements of the embryo, gametophyte, or both *(16)*. There is a strong genetic component to seed germination with high family heritability. Both fresh seed and stored seed require cold stratification temperatures of 1° C (33° F) to 5° C (41° F) to break dormancy. Germination is epigeal. The seeds of western white pine usually germinate in the spring in soil that was wet to field capacity by melting snow. In the Inland Empire, seed germination at lower elevations begins in late April. At higher elevations and on protected sites, germination may be delayed until early June. Germination can continue on exposed sites until July 1 and on protected sites until August 15. Under full sun, germination begins much earlier and ends much earlier than in partial or fully shaded conditions. Soil temperatures probably control the beginning of germination, and drying out of the topsoil or duff probably stops germination *(28)*. Light appears to have little importance in natural germination of western white pine seed. Mineral surfaces are better germination media than duff even though duff may contain many stored seeds.

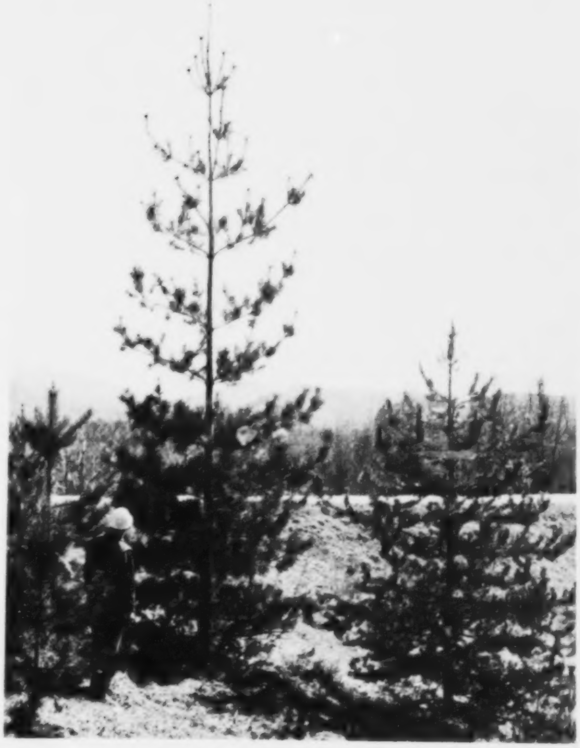

Figure 3—*A western white pine showing rate of growth and branching habit.*

During the first growing season, a high percentage of seedlings die, principally because of diseases, but insects, rodents, and birds cause serious seedling losses. *Fusarium*, cause of a damping-off disease, and *Neopeckia coulteri*, a snow mold, can cause extensive seedling mortality during the first year *(15)*. Seedlings up to 5 years old are often killed by *Rhizina undulata*, a root rot, in patches 0.5 m (1.6 ft) to 1.5 m (5 ft) in diameter. Seedling mortality late in the first growing season is due primarily to temperature and drought. High surface temperature is the most important cause of mortality on exposed sites, and drought is a factor on heavily shaded areas where root penetration is slow and unable to keep pace with receding soil moisture. For the most part, western white pine seedlings have low drought tolerance *(20)*.

All factors considered, western white pine seedling establishment is favored by partial shade on severe to moderately severe sites. On the more sheltered sites, such as north slopes, little or no shade is best for seedling establishment *(28)*. Once established, western white pine grows best in full sunlight on all sites.

Early root and shoot growth of western white pine seedlings usually is not rapid. The first summer, the primary root grows about 15 cm (6 in) to 30 cm (12 in) in open situations, between 13 cm (5 in) and 23 cm (9 in) under partial shade, and only 5 cm (2 in) to 8 cm (3 in) under full shade. Seedlings planted in soils rich in nutrients, high in organic matter, and with low bulk densities can have first-year root elongation up to 50 cm (20 in). Seedlings usually average between 3 cm (1 in) and 5 cm (2 in) in height by the end of the first growing season. In the Inland Empire, open-grown western white pine seedlings require about 8 years to reach a height of 1.4 m (4.5 ft) *(28)*. Similarly, 20-year-old western white pine (fig. 3) grow about 81 cm (32 in) to 99 cm (39 in) per year on good sites and about 23 cm (9 in) to 46 cm (18 in) on poor sites.

Both height growth and diameter growth of western white pine in the Inland Empire usually begin about the first week of May but may begin as early as April 5 and as late as June 25 depending on elevation, latitude, and aspect *(24)*. Also, in the Inland Empire, leaf buds usually open near May 21 but may open as early as March 27 and as late as June 21. Here, shoot growth usually ends by August 11; reported dates for shoot growth cessation are as early as June 9 and as late as October 21. Winter buds can be formed as early as June 14 and as late as September 30 but are usually formed by August 13. In the Inland Empire, diameter growth normally ceases by the end of August. Old needles usually turn straw yellow between the middle of August and the first week of September and drop soon thereafter. Total needle fall of western white pine is moderate when compared to associated species *(20)*, with needle retention of 3 to 4 years.

Table 1—Average size and volume of dominant and codominant western white pine growing in fully stocked stands in the Inland Empire

Item	Site index at base age 50 years		
	12.2 m or 40 ft	18.3 m or 60 ft	24.4 m or 80 ft
Dominants and codominants			
D.b.h., cm	29.5	41.9	56.9
Height, m	26.8	40.2	53.3
Volume, m^3	0.8	2.2	4.9
Cubic volume,[1] m^3/ha	699	976	1,267
Basal area, m^2/ha	70	72	74
Dominants and codominants			
D.b.h., in	11.6	16.5	22.4
Height, ft	88.0	132.0	175.0
Volume, ft^3	27.5	77.0	171.6
Cubic volume, ft^3/acre	9,980	13,950	18,100
Basal area,[1] ft^2/acre	306	314	322

[1] In trees 0.2 cm (0.6 in) and larger in d.b.h.

Vegetative Reproduction—Western white pine does not naturally reproduce by sprouting or layering. Cuttings from trees more than 4 to 5 years old are difficult to root *(3)*, although cuttings from 3-year-old seedlings have been rooted with fair success using rooting hormones. Needle bundles from 2-year-old seedlings have produced roots and some have produced shoots successfully.

Western white pine is relatively easy to propagate by grafting at all ages *(3)*. Several types of grafts have been used; early spring grafting before flushing has been most successful. Also, scions, taken from a variety of places in the tree crown, graft with equal success. Grafting conducted under greenhouse conditions is more successful than field grafting. Interspecies grafting on other five-needle rootstocks, such as eastern white pine *(Pinus strobus)*, sugar pine *(P. lambertiana)*, and blue pine *(P. griffithii)*, has been generally successful. Grafting of western white pine on species other than the five-needle white pines has not been accomplished.

Table 2—Mean annual increment of fully stocked stands of western white pine in the Inland Empire

Age	Site index at base age 50 years		
	12.2 m or 40 ft	18.3 m or 60 ft	24.4 m or 80 ft
yr		*m^3/ha*[1]	
20	0.84	1.40	1.89
40	3.29	4.62	5.95
60	4.90	6.86	8.89
80	5.67	7.84	10.29
100	5.88	8.26	10.78
120	5.81	8.12	10.57
140	5.53	7.70	9.94
yr		*fbm/acre*[1]	
20	12	20	27
40	47	66	85
60	70	98	127
80	81	112	147
100	84	118	154
120	83	116	151
140	79	110	142

[1] In trees 0.2 cm (0.6 in) and larger in d.b.h.

Sapling and Pole Stages to Maturity

Growth and Yield—Western white pine trees most often have clean boles with minimum taper and narrow crowns. In the absence of western white pine blister rust (*Cronartium ribicola*), the species is long lived; trees are commonly 300 to 400 years old and rarely, up to 500 years old. Overmature trees are often more than 180 cm (71 in) in d.b.h. and 60 m (197 ft) tall.

Tables 1 and 2 show the sizes, net volume, basal areas, and growth rates for western white pine in fully stocked stands in the Inland Empire. Although blister rust modifies stand development, in the absence of the rust, stands develop as shown.

Rooting Habit—The extent of western white pine's root system and the density of its rootlets depend on external conditions (*18*). Approximately 65 percent of the total root system, exclusive of the central vertical system, occurs in the uppermost 30 cm (12 in) of soil. Mature western white pine systems can spread 8 m (26 ft) laterally from the root collar with verticals descending off the lateral system, as well as in a concentration beneath the root collar. The root systems are tolerant of dense soils and have moderate growth rates. Western white pine trees have approximately 75 percent of their absorbing surface in the upper 60 cm (24 in) of the soil (*28*). Fine root development of western white pine is favored where vegetative competition is low and available moisture is high.

The fungi that have been reported to form mycorrhizae with western white pine are *Suillus granulatus*, *S. subaureus*, *S. subluteus*, *Boletellus zelleri*, *Cenococcum graniforme*, *Gomphidius ochraceus*, *G. rutilus*, *Russula delica*, *R. xerampelina*, and *Tricholoma flavovirens*.

Reaction to Competition—Western white pine is almost always a seral species. It is classed as intermediate in shade tolerance when compared to other northwestern tree species. The species attains a dominant position in the stand only following wildfires, even-aged silvicultural systems, or through cultural stand treatments favoring the species.

Western white pine can be regenerated using even-aged silvicultural systems. On favorable sites, clearcut, seed-tree, and shelterwood systems result in adequate and diverse natural regeneration within 5 to 10 years after the regeneration cut. If a natural blister rust-resistant seed source is not present on the site, planting can be used to regenerate the stands.

Western white pine seedlings are well suited for planting. Both bare-root and container-grown western white pine seedlings have excellent survival and growth when properly planted on appropriate sites. Bare-root stock has better survival with spring planting, but containerized stock appears to have excellent survival when planted during either season.

When natural regeneration and the clearcut system are used for establishing conifer mixtures that include western white pine, it is not uncommon to regenerate 11,000 trees per hectare (4,451/acre), of which 1,000/ha (405/acre) are western white pine (*4*). Similarly, seed-tree cuts can produce 12,000 trees per hectare (4,856/acre) of which 1,500/ha (607/acre) are western white pine. Shelterwood systems produce more trees, but the proportion that are western white pine is less than for other systems. On southerly aspects, regardless of the cutting system, less regeneration occurs.

The individual tree selection system cannot be used to manage western white pine successfully because it tends to favor the more shade-tolerant species, such as western redcedar and western hemlock, but group selection may have limited application.

Where reproduction has become established under partial cuttings, the density of overstory and time until removal greatly affect development. Western white pine growth can be inhibited even by the shade of a light shelterwood. Sixteen-year-old western white pine growing under an overwood density of 6 m^2/ha (27 ft^2/acre) were 2.0 m (6.6 ft) tall compared to trees 0.5 m (1.6 ft) tall growing under an overwood density of 21 m^2/ha (91 ft^2/acre) (*28*).

The composition of a western white pine stand is determined during the first 30 years of the stand's life (*13*). Lodgepole pine and western larch can grow one and one-half times as fast in height as western white pine during this period. Western larch can usually maintain its superiority in height growth through maturity, but lodgepole pine's growth superiority seldom lasts past age 50. Similarly, grand fir can equal western white pine height growth for the first 30 years and Douglas-fir is about equal in height growth. On northerly aspects and in shaded conditions, western hemlock height growth can equal that of western white pine (*8*).

Dominant western white pine over age 30 responds to release, but not aggressively. In the Inland Empire, in 55- to 65-year-old stands, half of the basal area must be removed to gain lasting improvement (*10*). The effectiveness of light to moderate thinnings in 55- to 65-year-old stands of western white pine is short-lived. Therefore, during the first 30 years, species composition is relatively plastic and can be modified materially by changing the density of residual overwood and by weeding or thinning. Beyond age 30, treatments are less effective and must be drastic to be long lasting.

Damaging Agents—At one time or another, fire has left its mark on practically every part of the western white pine forest *(28)*. Western white pine depends on fire or timber harvesting to remove competing conifers and allow it to become established as an early seral species. Its relatively thin bark and moderately flammable foliage make it intermediate in fire resistance among its conifer associates *(20)*. As a result of fire protection and the lack of major fires, plus blister rust infection, the proportion of western white pine regeneration (planted and natural) in northern Idaho, eastern Washington, and western Montana decreased from 44 percent in 1941 to 5 percent in 1979.

Western white pine when dormant is tolerant of cold and along with lodgepole pine is one of the more frost-tolerant northwestern species. Needle desiccation can occur when cold, drying winds cause excessive loss of moisture that cannot be replaced fast enough because of cold or frozen soil or tree trunks. Also, western white pine is more tolerant of heat than most of its more shade-tolerant associates.

The species is sensitive to both sulfur dioxide and fluoride smelter fumes, which cause the foliage to yellow and drop prematurely *(15,20)*. Depending on the site, western white pine is relatively windfirm, but considerable damage can occur from windthrow. Snow often causes breakage in young pole stands.

Western white pine is beset by many serious diseases *(15)*. By far the most prominent disease of western white pine is blister rust. In northern Idaho and contiguous parts of Montana and Washington, a combination of climate, abundant alternate host plants (species of *Ribes*), and susceptible pines contribute to heavy losses. But, through selection of naturally rust resistant trees for seed sources for natural regeneration and planting of rust resistant nursery stock, damage to western white pine stands from blister rust in the future should be minimal. Other stem diseases, such as dwarf mistletoe, *Arceuthobium laricis*, and *A. tsugense*, occur on western white pine; however, they are of little consequence.

In prolonged periods of drought, pole blight, a physiological disorder, can occur in stands of the 40- to 100-year class, causing yellow foliage and dead resinous areas on the trunk. Later the top dies and, in a few years, the tree. The disease does not appear to be caused by a primary pathogen but results from rootlet deterioration in certain soils restricting the uptake of water. The disease, a consequence of a drought from 1916 to 1940 *(19)*, caused serious mortality to western white pine from 1935 to 1960. At present, the disease is not a major cause of mortality in western white pine stands. In conjunction with pole blight studies, root lesions caused by *Leptographium* spp. were isolated; these could have a role in the decline caused by pole blight.

A needle blight, caused by *Lecanosticta* spp., often leads to shedding of foliage more than 1 year old. Another foliage disease that attacks mainly the upper and middle crown is needle cast caused by *Lophodermella arcuata*. Two other needle cast fungi, *Bifusella linearis* and *Lophodermium nitens*, attack isolated trees.

The foremost root disease of western white pine is *Armillaria* spp., causing fading foliage, growth reduction, root-collar exudation of resin, dead and rotten roots, and black rhizomorphs. *Heterobasidion annosum* and *Phellinus weiri* also cause some mortality of individuals and groups. The most important butt-rot fungi are *Phellinus pini*, *Heterobasidion annosum*, and *Phaeolus schweinitzii*. Many other fungi are capable of causing decay in injured or overmature trees, and rot often becomes excessive in trees over 120 years of age.

The bark beetles are the most important group of insects that attack western white pine. The mountain pine beetle *(Dendroctonus ponderosae)* kills groups of trees, primarily in mature forests. Trees weakened by blister rust are often attacked by the mountain pine beetle. Likewise, weakened trees are sometimes attacked by the red turpentine beetle *(Dendroctonus valens)*. Usually, this beetle is not aggressive and does not become epidemic, but through repeated attacks it can kill trees. More often, it just weakens them, leading to fatal attack by other bark beetles *(12)*.

Attack of western white pine by mountain pine beetle sometimes results in attack on the bole by emarginate ips *(Ips emarginatus)*. Likewise, the ips beetle *(Ips montanus)* attacks weakened western white pine, its principal host, in association with other bark beetles. The *Pityogenes fossifrons* beetle breeds principally in western white pine, but its attacks are seldom primary. The beetle is capable, however, of attacking western white pine reproduction. Many other bark beetles and insects attack western white pine, but, for the most part, they do not cause extensive damage.

Special Uses

Because western white pine wood is nonresinous, it is highly desired for the manufacture of moldings and trim. Also, western white pine is used for pattern stock, in cabinet shops, and for home handicraft because of its softness and workability. The clear grades of lumber are used for patterns in the foundry industry, mainly because of the high degree of dimensional stability. Decorative plywood is manufactured by slicing, and a limited amount of rotary-cut veneer is manufactured for industrial use.

Western white pine grows in some of the finest western outdoor recreation areas and has considerable esthetic value. In addition, the long, distinctive cones are collected in considerable numbers for novelties or souvenirs.

Genetics

Population Differences

Western white pine is different in genetic variation from most other conifers that have been intensively studied *(26)*. Within northern Idaho, western white pine genetic variation is high, and most of this variation is among trees within a stand. Differences among stands and elevational zones occur, but the proportion of the variance attributable to these sources is usually smaller than that for trees within stands. Evidence indicates little geographic or ecologic differentiation of populations for western white pine. The adaptation of western white pine to different geographic, climatic, topographic, and edaphic conditions is governed more by phenotypic plasticity than by selective differentiation *(22)*. Also, it appears that there is little difference among populations from coastal Washington and western British Columbia and northern Idaho populations *(27)*. There appear to be genetic differences, however, between California populations and Idaho populations *(23)*. Because of the small genetic variation detected in populations of western white pine in northern Idaho, seeds can be transferred without regard to elevation, latitude, longitude, or habitat type.

Races

Several single recessive genes are recognized in western white pine *(3)*. Albino genes, chlorophyll deficient genes, a curly foliage gene, and a dwarfing gene have been found. Monoterpenes also appear to be under strong genetic control. Height growth gains of 4 to 12 percent are possible according to estimates from progeny testing and selections.

Work on inheritance of blister rust resistance in western white pine began in 1950. This early work indicated considerable heritability of blister rust resistance. Most foliar resistance is governed by genes reducing the frequency of secondary needle infections and causing slow fungus growth in secondary needles *(3)*. In the stem, genetic resistance is governed primarily by genes controlling a fungicidal reaction and causing slow growth of the fungus. Other resistance mechanisms include lowered frequency of needle lesions, premature shedding of needles, and fungicidal reaction in the short shoot. Nursery and field tests of rust resistant seedlings after two cycles of selections indicate rust resistance of 66 and 88 percent, respectively.

Hybrids

Western white pine can be easily crossed with other five-needle white pines *(3)*. It hybridizes successfully with Balkan pine *(Pinus peuce)*, blue pine *(P. griffithii)*, eastern white pine *(P. strobus)*, Japanese white pine *(P. parviflora)*, southwestern white pine *(P. strobiformis)*, and limber pine *(P. flexilis)*. Hybridization with Swiss stone pine *(P. cembra)*, Korean pine *(P. koraiensis)*, and whitebark pine *(P. albicaulis)* has not been as successful.

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Pinus nigra Arnold European Black Pine

Pinaceae Pine family

David F. Van Haverbeke

European black pine *(Pinus nigra)*, also called Austrian pine, was one of the early tree introductions into the United States, first reported in cultivation in 1759 *(52)*. Black pine was one of the first conifers tested for adaptability in the Sandhills of Nebraska in the 1891 Bruner plantation, Holt County, and in 1909 on the Nebraska National Forest. It was also planted by homesteaders on the Great Plains in the early 1900's to provide beauty and protection from wind and snow on the treeless prairies (fig. 1).

The most common seed sources of European black pine introduced into the United States have been from Austria and the Balkans *(69)*. Sources from other parts of the natural range are relatively scarce in this country, except in a few arboreta. The best of these, however, grow as much as 50 percent faster than the typical Austrian sources. Today, European black pine is one of the most common introduced ornamentals in the United States.

Habitat

Range

European black pine is native to Europe. Its range extends from longitude 5° W. in Spain and Morocco to about 40° E. in eastern Turkey; and from latitude 35° N. in Morocco and Cyprus to 48° N. in northeastern Austria and to 45° N. latitude in the Crimea, U.S.S.R. *(11)*. Black pine grows widely throughout southern Europe from the eastern half of Spain, southern France, and Italy to Austria; south throughout Yugoslavia, western Romania, Bulgaria, and Greece on the Balkan Peninsula; east to southern Russia in the Crimea and south to Turkey; and on the islands of Cyprus, Sicily, and Corsica, with outliers in Algeria and Morocco *(40)*.

Black pine is hardy in southern Ontario and New England, the North Central United States, and in parts of the West; and, along with Scotch pine *(Pinus sylvestris)*, Japanese black pine *(P. thunbergii)*, and Japanese red pine *(P. densiflora)*, it is reported to have become naturalized in parts of New England and the Lake States *(72)*. Its escape from cultivation locally in the northeast, and west to Missouri, is acknowledged, but it is not generally recognized as having become naturalized *(36)*.

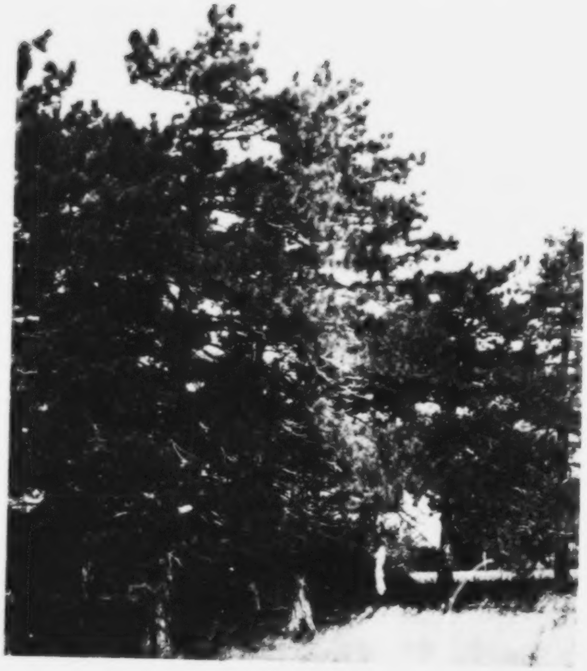

Figure 1—*European black pine, an 18th century introduction into the northeastern United States.*

The ecotypic variation in wide-ranging species such as *P. nigra* normally includes sufficient morphological variation that taxonomists have recognized many nomenclaturally distinct species, subspecies, or varieties to describe this variation. In this paper, for simplicity, the species are referred to by geographic origin, for example, European black pine or black pine from Austria, the Balkans, or Corsica, rather than by subspecies or varietal names. For synonymy see the Genetics section.

Climate

In parts of its native European habitat, black pine grows in a cool to cold temperate climate *(23)*. The northern varieties are very frost-hardy, withstanding temperatures of -30° C (-22° F), and the southern varieties tolerate -7° C (19° F) temperatures. Annual precipitation varies from 610 to 1020 mm (24 to 40 in). The species has been shown to carry on

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photosynthesis at –5° C (23° F), with respiration still detectable at –19° C (–2° F) *(21)*. Black pine withstands the weight of ice well and is considered hardy except in the coldest, hottest, and driest regions.

In the United States, black pine is mainly suited to Climatic Zone IV, which includes most of Nova Scotia, southern Maine, New Hampshire, Vermont, New York, southern Ontario, Michigan, northern Indiana, northern Illinois, Wisconsin, Iowa, northern Missouri, Nebraska, Kansas, Colorado, Utah, Idaho, Montana, southwestern Alberta, and central British Columbia *(52)*. It has either failed or has performed poorly in the southern states of Oklahoma, Texas, North Carolina, Georgia, northern Florida, and Arkansas.

Soils and Topography

European black pine is adapted to many soil types and topographic habitats. In its native range the species commonly is separated into three geographic groupings: western, central, and eastern. Sources from southern France and Spain, the western group, often are indifferent to soil type; sources from Corsica, Italy, and Sicily, the central group, grow poorly on limestone soils; while sources from the Balkans and the Crimea, U.S.S.R., the eastern group, appear to do well on the poorer limestone soils *(31)*. Black pine also grows well on podzolic soils *(8)*.

In England, Austrian material does well as a shelterbelt tree in exposed situations near the sea on light, dry, shallow soils, sands, chalks, and limestone. It is less well-suited than Corsican strains in infertile, "stiff," or wet soils *(6)*.

Although European black pine often is found on poor, calcareous, sandy, and even pure limestone soils, it requires a deep soil. On good sites, Italian, Sicilian, and Corsican strains are fast growing (up to 40 m or 131 ft tall) and straight *(23,40)*.

In Europe, black pine is found at elevations ranging from 250 to 1800 m (820 to 5,910 ft). In Austria, it is found on poor dolomite and limestone sites from 260 to 500 m (850 to 1,640 ft) and on good soils from 300 to 700 m (980 to 2,300 ft); at about 610 m (2,000 ft) in the Dinaric Alps of the Balkans; at 1200 m (3,940 ft) in the Sierra de Segura of southeastern Spain; and from 900 to 1800 m (2,950 to 5,910 ft) on Corsica *(40)*.

In the United States the major experience with European black pine has been with Austrian sources. Most planting stock is provided by private nurseries, and several million trees are produced annually in the Northeastern States. The species has been especially successful in the Northeast on soils of high pH in the southern part of the area formerly planted to red pine *(Pinus resinosa) (69)*. There is evidence, however, that black pine is not a good choice to replace red pine on many northeastern sites *(42)*. After 21 growing seasons, black pine averaged about 2.1 m (7 ft) shorter and 3.2 cm (1.25 in) less in d.b.h. on several New York soil types.

In the Great Plains region, European black pine is not a demanding species and is being planted on soils of the orders Aridisols, Entisols, Mollisols, and Vertisols. More specifically it grows well throughout a broad range of soils including sandy loams, silty clays, and calcareous soils. It is about as adaptable to most Great Plains windbreak and shelterbelt sites as ponderosa pine *(Pinus ponderosa)*, although on the very poor sites it suffers considerable mortality. Once established, however, the rate of height growth is good, and density and form of the crown are superior to ponderosa pine *(50)*. Survival, height, vigor, and crown development throughout the Great Plains region are best in deep, permeable, well-drained, and mostly sandy loams along river lowlands and stream valleys where the water table is 6.1 m (20 ft) or less below the surface; they are poorest on shallow, sandy, or silty soils underlain by claypan or gravel.

After early success in the turn of the century plantings in the Nebraska Sandhills, black pine was not considered as desirable for extensive plantings as eastern redcedar *(Juniperus virginiana)*, jack pine *(Pinus banksiana)*, or ponderosa pine. In Iowa, black pine was reported to be tolerant of high-lime soils, where survival and growth were best on western and northern exposures *(19)*.

Associated Forest Cover

European black pine in its many forms grows naturally throughout the Mediterranean region in association with Scotch pine, Swiss mountain pine *(Pinus mugo)*, Aleppo pine *(P. halepensis)*, Italian stone pine *(P. pinea)*, and Heldreich pine *(P. heldreichii) (11,40,69)*. Other pine species that share the same geographic range or portions of it with European black pine include Swiss stone pine *(P. cembra)*, Balkan pine *(P. peuce)*, maritime pine *(P. pinaster)*, and *P. brutia* and its variant *P. pithyusa* *(11)*. In England some naturally regenerating European black pines, from principally Corsican sources, are associated with birch *(Betula pendula)*, willows *(Salix caprea* and *S. cinerea)*, and oak *(Quercus robur)* on the sand dunes, saltmarshes, and intertidal sand and mudflats of the north Norfolk coast *(27)*.

In the United States, European black pine is associated with numerous species consequent to its use in landscape and environmental plantings. Its apparent tendency to escape, possibly to naturalize, and to hybridize with certain other pines may, in time, result in some natural species associations in this country.

Life History

Reproduction and Early Growth

Flowering and Fruiting—European black pine is monoecious, with staminate (microsporangiate) and ovulate (megasporangiate) strobili borne separately on the same tree *(67)*. Staminate strobili, clustered at the base of new shoots, mostly on older lateral branches in the lower crown, are cylindrical, short-stalked, bright yellow, about 2 cm (0.8 in) long with numerous scales, and contain pollen in great quantity *(12,49,52)*.

One or two ovulate strobili (conelets) emerge near the end of the new growth of terminal and lateral branches; they are cylindrical, small, bright red, and short-stalked or sessile *(12,49,67)*. Pollen dispersal and conelet receptivity occur from May to June. Individual ovulate conelets are receptive for the pollen for only about 3 days, however *(67)*. After pollen dispersal, the staminate strobili dry and fall within several weeks. The scales of the ovulate strobili close within a few days of pollination, and the conelets begin a slow developmental process. At the beginning of the second growing season, the ovulate strobili are only about 2 cm (0.8 in) long *(47)*. Fertilization takes place in the spring or early summer about 13 months after pollination, and the cones, now turned green in color begin to grow rapidly from about May until maturity in the fall *(67)*.

The fruit, a tough, coarse, woody, yellow-green cone during the preripening second summer, changes to shiny yellow-brown to light brown at maturity from September to November of the second growing season *(12,49,52)*. Cones are descending, sessile, ovoid, and 5 to 8 cm (2 to 3 in) long. Cone scales are shiny, thickened at the apex, and end in a short spine on the dorsal umbo.

Minimum seed bearing age is 15 to 40 years *(40,52,67)*. In England, black pine from Corsican sources produce their first heavy cone crops at ages 25 to 30 years and reach maximum production between 60 and 90 years of age *(27)*. The interval between large cone crops is 2 to 5 years.

Seed Production and Dissemination—Seeds are dispersed from October through November of the second growing season. Seeds are reddish brown, often mottled, 6.4 mm (0.25 in) long at one end of a membranous wing 19 mm (0.75 in) long *(49)*. Two winged seeds are produced on the upper surface of each scale of the cone except for those at the tip and base.

Seeds are extracted from harvested cones by air-drying for 3 to 10 days or kiln-drying at 46° C (115° F) for 24 hours. Sound seeds are separated from empty seeds by flotation in 95 percent ethanol *(31)*. The number of sound seeds per cone in Austrian black pine ranges from 30 to 40, of which 15 to 20 are germinable *(67)*.

Cleaned seeds average 57,300 per kilogram (26,000/lb) with a range from 30,900 to 86,000/kg (14,000 to 39,000/lb). Seeds from the Crimea, Turkey, and Cyprus tend to be the largest, ranging from 38,600 to 45,900/kg (17,500 to 20,800/lb), and those from Corsica the smallest, ranging from 61,700 to 79,400/kg (28,000 to 36,000/lb) *(31,67)*.

Seedling Development—European black pine is easily grown from seed and transplants well. Fresh seeds require no pre-sowing stratification; but stored seeds can be cold-stratified up to 60 days to hasten germination. Ninety-nine percent germination was obtained from seeds stored 10 years in closed containers at 6.6 percent moisture content (ovendry-weight basis) at 0° to 2° C (32° to 36° F). No loss of viability occurred in seeds stored in sealed containers at room temperature after 2 years. Storage at moisture contents as low as 2 percent or as high as 12 percent, however, was detrimental to seeds stored for long periods *(25)*. A light period of 8 hours at 30° C (86° F) and a dark period of 20° C (68° F) for 16 hours is recommended for germination *(24)*. Germination is epigeal *(31)*. Seeds from Corsican sources tend to germinate more slowly than those from Austria and Calabria *(55)*.

In nurseries, nonstratified seeds are sown in the fall or spring, at a density to obtain 540 to 650 seedlings per square meter (50 to 60/ft^2). Seeds should be sown at a depth of 13 to 19 mm (0.5 to 0.75 in).

Black pine seedlings can be produced in peat-perlite containers using low rates of fertilizers (e.g. Osmocote 18 N–2.6P–10K) *(1)*. Experiments with 3-year-old nursery seedlings from 27 different European provenance locations demonstrated that nitrogen and manganese ion uptake was significantly enhanced, but that uptake of potassium, phosphorus, magnesium, boron, zinc, and aluminum ions was suppressed by 45 percent urea *(33)*. Application of a pre-emergence herbicide was found to enhance mycorrhizal formation in nursery-grown seedlings *(61)*.

In Germany, seedlings of all provenances of black pine from Corsica, Spain, and southern France suffered severe frost damage in the nursery, and those from southern Italy suffered some damage; but seedlings from eastern provenances (Austria, Yugoslavia, Greece, and Cyprus) were undamaged *(54)*. Experience in the United States strongly suggests that black pine seed be obtained from the Balkan Peninsula or from the Crimea, for improved winter hardiness *(32)*.

Nursery-grown seedlings are commonly field-planted as 2-0, 2-1, or 2-2 seedlings. Field-plantable seedlings can be greenhouse grown in containers in 9 months following a predetermined schedule of temperature, moisture, relative humidity, and nutrient application *(62)*.

In England, germination success of direct-sown Corsican black pine seed was found to be strongly dependent on aspect; satisfactory germination was achieved on north-facing slopes on young sand dunes nearest the sea *(27)*. Newly germinated seedlings suffered very heavy losses from voles and rabbits but became unpalatable to them within 2 months.

Vegetative Reproduction—At present, grafting is the most common method for vegetatively propagating European black pine. Needle fascicles have been rooted, but only fascicles from 1-year-old short shoots on young (5-year-old) plants were able to form callus or to root. Propagation by cuttings and air-layering has not been reported.

The side graft method is the usual practice, but cleft and veneer grafts can also be used. Grafting is done on actively growing stock, and removal of the stock by pruning must be gradual after scion growth begins.

Stock–scion incompatibility in black pine is not a serious problem, especially if the stock and the scion are of the same race. Black pine can be grafted onto *Pinus sylvestris, P. resinosa, P. khasya, P. montana, P. mugo,* and *P. contorta*; but semi-incompatibility has been found with *P. ponderosa, P. radiata,* and *P. armandii (67)*.

Research in Yugoslavia indicates that a wide range of auxin concentrations, can promote the development of rootable plantlets from shoot tip explants *(30)*.

Sapling and Pole Stages to Maturity

Growth and Yield—European black pine transplants well when small, or when larger if transplanted in the dormant season *(49)*. It is a fast and vigorously growing tree of pyramidal form with full, dark foliage. In England, its habit has been described as bushy in youth, presenting a coarse appearance and having poor stem form; this severely limits its timber value, although it grows rapidly, is hardy, and provides an excellent windbreak *(6)*.

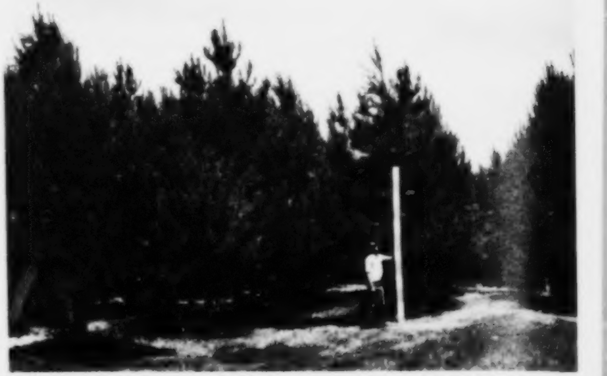

Figure 2—*Provenance tests, like this one in Nebraska, identify seed sources of European black pine best adapted to particular environments.*

In the Great Plains region black pine grows relatively rapidly during the first 20 years after planting—approximately 0.3 m (1 ft) per year on the average site *(57)*. Similar rates of growth have been reported in Iowa, where 12-year-old trees average 3.9 m (12.9 ft) in height *(19)*. The fastest growing source in a Nebraska provenance study, a disease resistant source from Yugoslavia, was 5.9 m (19.4 ft) tall at age 12 *(51)* (fig. 2) and 9.7 m (31.8 ft) tall at age 20 *(64)*. Average heights of 4.4 m (14.5 ft) and diameters of 13.5 cm (5.3 in) were recorded in a 15-year-old Michigan provenance plantation *(68)*.

The average growth rate of European black pine in Great Plains shelterbelts decreases 7.6 cm (3.0 in) per year from about age 20, so that annual height increase is only 6.1 to 9.1 cm (2.4 to 3.6 in) 50 years after planting. Height growth in the Loess Plains of Nebraska compares favorably with height growth in Europe up to age 50. Height growth in Europe, however, is slower during the early years and faster after 40 to 50 years *(57)*.

A 25-year-old stand of planted black pine in Michigan State University's Kellogg Forest is similar in growth to red pine stands on the same forest and, like them, is being thinned for pulpwood and pruned for timber production *(69)*. Use of faster growing black pine sources does not cause the production of lower wood quality *(34)*.

Forest plantings established in the North Central and Northeastern United States during recent decades are generally thrifty. Data on growth of older stands, however, is limited to a few relatively small plantings, such as the group of 50-year-old trees in the University of Michigan's Nichols Arboretum at Ann Arbor. These trees are similar in growth rate to nearby red pine, Scotch pine, and eastern white pine (*P. strobus*) *(69)*. European black pine, in the Secrest Arboretum at Ohio State University's Agricultural Research and Development Center in Wooster, OH, has performed as follows *(3)*:

Age	Average d.b.h.		Average height	
yr	*cm*	*in*	*m*	*ft*
10	9.7	3.8	5.3	17.4
13	10.7	4.2	6.3	20.6
19	14.2	5.6	9.6	31.5
24	16.0	6.3	11.7	38.5
25	18.0	7.1	11.8	38.8
31	17.8	7.0	14.5	47.7
40	22.4	8.8	17.1	56.0
45	24.1	9.5	17.6	57.7

At age 45, the above trees would produce about 0.4 m^3 (14 ft^3) of wood per tree.

Height growth of Corsican material in England was proportional to the preceding winter's rainfall from October to March if soil moisture was below field capacity, and volume increment was proportional to the preceding year's height growth. Diameter growth began when the mean 5-day temperature rose to 10° C (50° F) and ended when the mean temperature fell below 10° C (50° F) *(56)*. Wood density of Corsican black pine grown in England was higher than that of other commercially grown exotics, and resin contents as high as 20 percent were found in the heartwood of individual trees *(10)*.

European black pine matures at about 80 years of age, commonly developing a flat, round, or spreading crown. The species attains heights of 20.1 to 50.3 m (66 to 165 ft) *(52,69)*. Minimum rotation periods of 160 to 180 years have been reported for black pine in Corsica, 240 to 360 years being the normal to produce trees 1 m (3.3 ft) in diameter *(12)*.

Rooting Habit—All varieties of European black pine are considered to be deep laterally rooted and, therefore, to perform best in deep soils *(22,49)*.

Reaction to Competition—European black pine is classed as intolerant of shade, and, therefore, must be planted in situations where it will receive full sunlight. Those from Austria and the Balkans have received increasing attention during recent decades from foresters and Christmas tree growers in the Northeastern United States as an alternative to red pine, which has been heavily damaged by the European pine shoot moth (*Rhyacionia buoliana*). It has proven especially successful on soils of high pH in the southern part of the area formerly planted to red pine *(69)*.

At Ithaca, NY, a series of four-paired, quarter-acre plots of red pine and black pine were established on a series of somewhat poorly drained to excessively well-drained acidic, silty loam, and other associated soils typical of New York's southern tier, to compare their performances. After 21 growing seasons, black pine averaged about 1.8 m (6 ft) in height and 3.2 cm (1.25 in) in diameter less than red pine over all sites. Branches were usually thicker and closer together, suggesting slower early height growth; stems suffered sapsucker damage, and the trees had many double forks and malformed shoots. These tests suggested that European black pine, from this source at least, was a poor choice to replace red pine on many northeastern sites *(42)*.

In the Great Plains shelterbelt planting, European black pine was frequently intermixed with ponderosa pine within the same row. Survival was about 5 percent better and height growth was about 0.7 m (2.3 ft) more for black pine over a 12- to 19-year period on the deep to medium, permeable, well-drained silty and sandy loams of loess origin *(50)*. Heights of trees also were more uniform within black pine rows because of freedom from damage by tip moths (*Rhyacionia* spp.). Density and form of crowns also were superior to ponderosa pine.

In West Virginia, 10 sources of European black pine, ponderosa pine, black locust (*Robinia pseudoacacia*), autumn olive (*Elaeagnus umbellata*), and European alder (*Alnus glutinosa*) were tested on strip mine spoils. Although all hardwood species grew faster than the pines, Yugoslavian sources grew faster and survived best of all other black pine sources *(29)*.

Damaging Agents—European black pine is susceptible to infection by many pathogens that damage seedlings, foliage, stems, and roots *(26)*. Damping-off and seedling root rots, caused by *Rhizoctonia solani, Phytophthora cactorum*, and *Pythium debaryanum*, and loss of seedling vigor caused by the dagger nematode (*Xiphinema americanum*) *(45)* are among the most common causes of seedling damage in nurseries.

Dothistroma needle blight, caused by the fungus *Dothistroma pini*, is one of the most damaging of the foliage diseases of black pine. The fungus has been found in 23 States in the United States and in three Provinces in Canada. Dothistroma needle blight is widespread and causes extensive damage to Austrian pine in Christmas tree plantings in Minnesota *(43)*, and in shelterbelt, ornamental, and Christmas tree plantings in the central and southern Great Plains *(48)*. Infection of current-year needles first occurs in mid-July, while infection of second-year needles begins in late May in the Great Plains and in British Columbia. Symptoms develop in early September to early November and consist of yellow and tan spots and bands that appear water-soaked on the needles. The bands and spots may turn brown to reddish brown, and the distal end of the needle becomes chlorotic, then necrotic, while the base of the needle remains green. Infected needles are cast prematurely *(46)*.

Genetic resistance to Dothistroma needle blight has been detected in European black pine. In a Nebraska test of 21 geographic sources *(51)*, some individual trees within 16 sources were highly resistant, while those from one Yugoslavian source showed universally high resistance *(48)*.

Lophodermium needle cast of pines, caused by *Lophodermium pinastri*, is a serious disease of European black pine in the Lake States, causing browning and premature dropping of needles and terminal bud dieback *(60)*. A needle disease caused by the fungus *Nemacyclus minor* has been reported from Pennsylvania *(38)*.

Diplodia tip blight, caused by the fungus *Diplodia pinea*, is a very damaging twig and stem disease of European black pine, especially to trees more than 30 years old. Entire new shoots are killed rapidly by the fungus. Trees repeatedly infected have some branches killed back to the main stem *(47)*.

Black pine seedlings in nurseries are susceptible to the fungi *Cylindrocladium scoparium* and *C. floridanum*. These fungi cause root rot, damping-off, and needle blight *(9)*.

Damage to black pine by insects and other pests is apparently of lesser consequence than that from fungal pathogens. The species has been reported to be injured by pine aphids, pine beetles, and pine weevils, but growing trees, on the whole, are relatively free from insect pests *(12)*. Damage by rabbits and sapsuckers has been noted *(19,42)*.

Some incidence of attack in northeastern United States from the Zimmerman pine moth *(Dioryctria zimmermani)*, the European pine sawfly *(Neodiprion sertifer)*, and the European pine shoot moth has been observed *(68)*.

Special Uses

European black pine is a widespread and important timber-producing tree of central and southern Europe, especially Corsica. The wood resembles Scotch pine but is rougher, softer in texture, and possesses less strength. Although the wood has a relatively larger proportion of sapwood to heartwood and thus requires a long rotation, it is used extensively throughout the Mediterranean region for general construction, fuelwood, and other purposes for which pine timber is needed *(12)*.

Elsewhere, black pine has been grown more for estate and landscape uses than as a timber crop, although in England during World War II it proved serviceable for box boards and pit props.

The species has been planted extensively in cold, semi-arid, exposed coastal regions for protection and sand dune fixation because of its capacity to withstand drought, to grow on light, dry sandy soils of low productivity, and to tolerate fill *(6)*. This frost-hardy, windfirm, and light-demanding species has been widely used for nearly 100 years in windbreaks and roadside plantings throughout the eastern Great Plains of the United States, where its dense foliage and stiff branches withstand wind, ice, and heavy snow.

The species has not been widely grown in the United States for timber production, although estate, school, and experimental plantings have been thinned for pulpwood and timber products *(69)*. It is occasionally tapped for resin, but its pitch is not as high in quality as that of slash pine *(Pinus elliottii)*.

European black pine is grown for Christmas trees in the North Central and Northeastern States *(34)* where it is not subject to heavy damage from the European shoot moth and tip moth, but where it is severely damaged by Dothistroma, Lophodermium, and Diplodia needle and tip blights.

It is being increasingly used in urban and industrial environmental improvement plantings because of its rapid growth and protoplasmic insensitivity to salt spray *(4)* and to industrial dust, dry soil, and smoke containing sulfur dioxide *(7)*. Excised shoots of black pine and other conifer species are capable of absorbing more SO_2, NO_2, and O_3 than shoots of a number of deciduous species *(18)*. It also provides wildlife habitat and might be used as a wood source *(39)*.

Genetics

Within the climatically and topographically diverse and disjunct distribution of European black pine, recognizable differences in the population have evolved through natural selection. As early as the third century B.C., Theophrastis (370–285 B.C.) recognized several striking variations within what is here called *Pinus nigra*.

Races and Varieties

The taxonomic record indicates that *Pinus nigra* is an extremely variable taxon, including more than 100 Latin specific, varietal, and formal names. Common names associated with the species include black pine, Austrian pine, "tsrnog bor," and "crnog bora." There is no general agreement on its nomenclature.

Among the several major treatments of the taxon, each based on solid work, there are differences in certain aspects *(5,12,13,14,15,22,52)*. Two commonly accepted authorities *(12,52)* are in general agreement, however, each partitioning the species into four varieties, the first of which describes the type:

Pinus nigra var. *austriaca* (Hoess) Aschers. & Graebn. (Austria to Balkan Peninsula) *(52)*
P. n. var. *nigra* Arnold (Austria, Yugoslavia, Hungary) *(12)*
P. n. var. *caramanica* (Loud.) Rehd. (Asia Minor) *(52)*
P. n. var. *caramanica* (Loud.) Rehd. (Crimea) *(12)*
P. n. var. *poiretiana* (Ant.) Aschers. & Graebn. (So. Europe) *(52)*
P. n. var. *maritima* (Aiton) Melville (Spain, Corsica, So. Italy, Greece) *(12)*
P. n. var. *cebennensis* (Gren. & Gord.) Rehd. (Pyrenees & So. France) *(52)*
P. n. var. *cebennensis* (Gren. & Gord.) Rehd. (Cevennes & Pyrenees) *(12)*

Blecić *(5)* treated European black pine as a series of subspecies as follows:

Pinus nigra ssp. *nigra* (Austria, Italy, Greece, Yugoslavia)
P. n. ssp. *salzmannii* (France, Northern Pyrenees, Central and Eastern Spain)
P. n. ssp. *laricio* (Corsica, Calabria, Sicily)
P. n. ssp. *dalmatica* (central region of the Yugolslav seaboard and neighboring islands)
P. n. ssp. *pallasiana* (Balkan Penninsula, Southern Carpathians, the Crimea)

Other treatments of the taxon have resulted in assignment of subspecies rank to segments of the population: *Pinus nigra* ssp. *occidentalis* with 6 named varieties, and *P. n.* ssp. *orientalis* with as many as 10 named varieties *(13)*. Recent genetic analyses of the European black pine population have added further refinements either confirming, expanding, or compositing the already established nomenclature *(2,32,33,54,55,67,68,69)*. Recent isoenzyme *(20,44)* and karyotic *(28)* analyses have further differentiated European black pine into identifiable groups.

Hybrids

Reports of natural hybridization between European black pine and other pine species in Europe include: *Pinus nigra* and *P. montana (58)*, *P. nigra* and *P. sylvestris (65)*, and *P. nigra* and *P. heldreichii* var. *leucodermis (22)*, although *P. heldreichii* is considered synonymous with *P. nigra* by many.

In the United States, natural hybridization has been reported between *Pinus nigra* and Japanese red pine (*P. densiflora*) in planted stands within close

Figure 3—*An outstanding specimen of European black pine, suitable for breeding.*

proximity of one another *(71)*; although research based on enzyme analyses, suggests that red pine cannot be the pollen donor in this naturally occuring putative hybrid *(41)*. Ninety-two percent of the seedlings derived from open-pollinated cones collected from the black pine stand were hybrids, and heterosis was evident in these seedlings. Cones yielded 22 filled seeds per cone. These are considered among the easiest of all tree hybrids to produce, providing the concentration of *P. densiflora* pollen in the pollen mix is very high *(63)*.

Early attempts at artificial crossing of European black pine with other pine species were mostly unsuccessful. Species included *Pinus resinosa, P. sylvestris, P. thunbergii, P. caribeae,* and *P. rigida (13,37,53)*.

Later, *Pinus nigra* was successfully fertilized by *P. resinosa* to produce progenies superior to either parent *(17)*. *P. nigra* has been reciprocally crossed successfully with *P. densiflora (35,66,70,71), P. sylvestris (65,70)*, and *P. thunbergii;* and with *P. tabulaeformis, P. taiwanensus (70)*, and *P. mugo (67)*.

In addition to the crosses shown above, the following combinations have been achieved using *P. nigra* and *P. sylvestris* as the mother tree:

P. nigra × *(P. thunbergii* × *densiflora)*
P. nigra × *(P. densiflora* × *nigra)*
P. nigra × *(P. nigra* × *densiflora)*
P. sylvestris × *(P. densiflora* × *nigra)*

The application of genetic principles, including testing and selecting adapted seed sources (provenances), followed by intraspecific and interspecific breeding of individuals selected from within adapted seed sources, promises further improvement in the form, disease resistance, vigor, and other economically important characteristics of *P. nigra* (fig. 3).

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Pinus palustris Mill. Longleaf Pine

Pinaceae Pine family

W. D. Boyer

Longleaf pine *(Pinus palustris)*, whose species name means "of the marsh," has been locally referred to as longstraw, yellow, southern yellow, swamp, hard or heart, pitch, and Georgia pine. In presettlement times, this premier timber and naval stores tree grew in extensive pure stands throughout the Atlantic and Gulf Coastal Plains. At one time the longleaf pine forest may have occupied as much as 24 million ha (60 million acres), although by 1985 less than 1.6 million ha (4 million acres) remained.

Habitat

Native Range

The natural range of longleaf pine (fig. 1) includes most of the Atlantic and Gulf Coastal Plains from southeastern Virginia to eastern Texas and south through the northern two-thirds of peninsular Florida. The species also grows in the Piedmont, Ridge and Valley, and Mountain Provinces of Alabama and northwest Georgia.

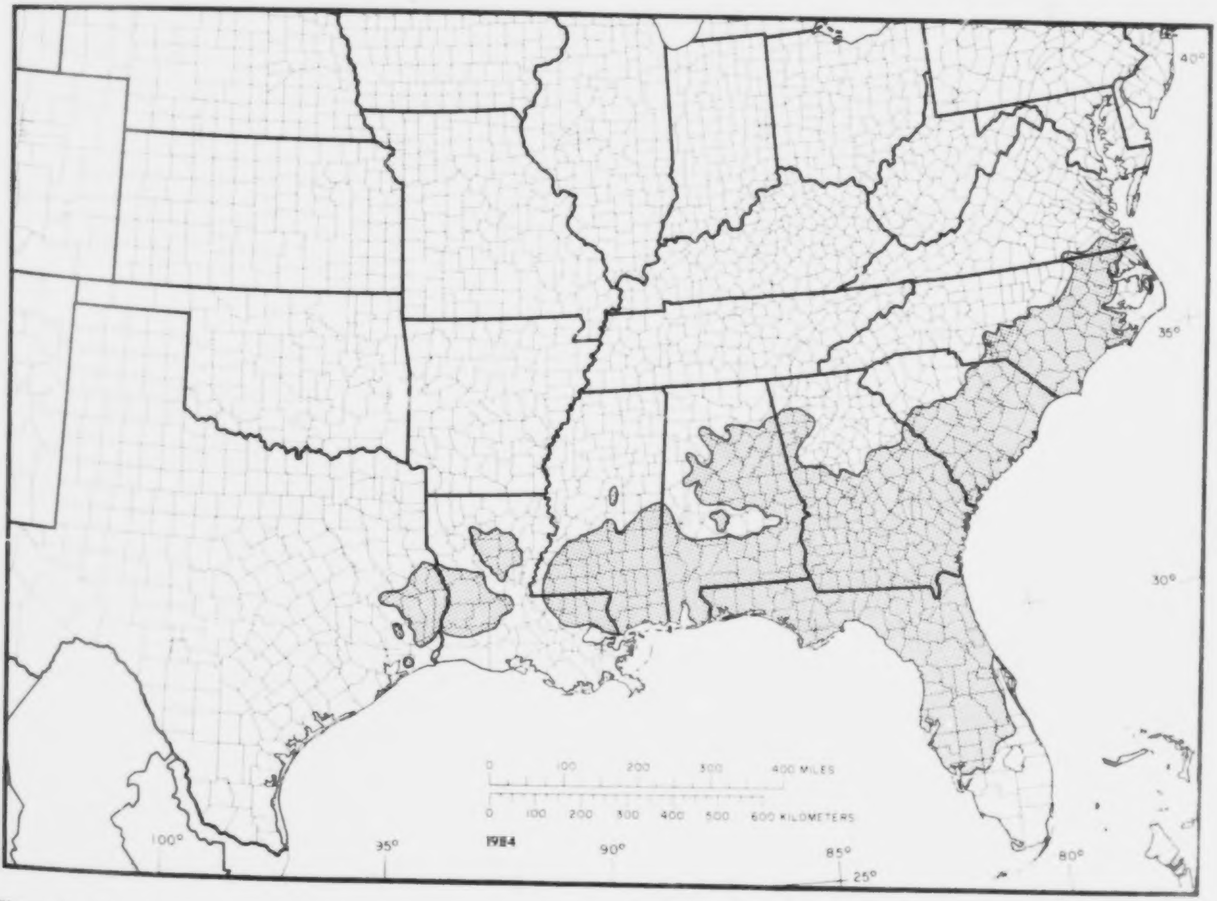

Figure 1—*The native range of longleaf pine.*

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Climate

Longleaf pine grows in warm, wet temperate climates characterized by hot summers and mild winters. Annual mean temperatures range from 16° to 23° C (60° to 74° F) and annual precipitation from 1090 to 1750 mm (43 to 69 in), the least being 1090 to 1270 mm (43 to 50 in) in the Carolinas and Texas and the greatest along the Gulf Coast of Alabama, Mississippi, and extreme west Florida. A distinct summer rainfall peak occurs along the Atlantic Coast, being most pronounced in Florida. A secondary rainfall peak in March becomes pronounced along the Gulf Coast. Fall is the driest season of the year, although droughts during the growing season are not unusual.

Soils and Topography

Longleaf pine is native to a wide variety of sites ranging from wet, poorly drained flatwoods to dry, rocky mountain ridges. Elevations range from barely above sea level near the beaches on the lower Coastal Plain up to about 600 m (1,970 ft) in the mountains of Alabama. Most of the longleaf pine forests are found on the Atlantic and Gulf Coastal plains at elevations below 200 m (660 ft). Here the soils are largely derived from marine sediments and range from deep, coarse, excessively drained sands to poorly drained clays. For the most part, surface soils are sandy, acid, low in organic matter, and relatively infertile. In the Mountain Province, soils are derived largely from granite, quartzite, schist, phyllite, and slate, while in the Ridge and Valley Province, soils are derived mostly from sandstone, shale, limestone, and dolomite *(21)*.

Within the natural range of longleaf pine, three soil orders are of major importance. Ultisols are the dominant order and cover most of the southeastern United States outside of peninsular Florida. Ultisols most commonly associated with longleaf pine are the Typic Paleudults and Plinthic Paleudults. The other two soil orders are Entisols and Spodosols. Deep, sandy Entisols, primarily Quartzipsamments, range from about 3 m (10 ft) above sea level in Florida up to about 185 m (600 ft) in Georgia and the Carolinas. Entisols have not developed diagnostic horizons. They make up the Sandhills of the Carolinas, Georgia, and northwest Florida and the sand ridges in the central Highlands of peninsular Florida. Spodosols, particularly Aquods, are typical of the flatwoods of the lower Coastal Plain in Florida. They are wet, sandy soils with a fluctuating water table that is at or near the surface during rainy seasons *(8)*.

Associated Forest Cover

The principal longleaf cover types are Longleaf Pine (Society of American Foresters Type 70), Longleaf Pine–Scrub Oak (Type 71), and Longleaf Pine–Slash Pine (Type 83) *(12)*. Longleaf pine is also a minor component of other forest types within its range: Sand Pine (Type 69), Shortleaf Pine (Type 75), Loblolly Pine (Type 81), Loblolly Pine–Hardwoods (Type 82), Slash Pine (Type 84), and South Florida Slash Pine (Type 111).

Longleaf pine develops in close association with periodic surface fires. The vegetation associated with longleaf pine reflects the frequency and severity of burning. In the past, frequent fires resulted in open, parklike stands of longleaf with few other woody plants and a ground cover dominated by grasses. Ground cover in longleaf pine in the Coastal Plains can be separated into two general regions, with the division in the central part of south Alabama and northwest Florida. To the west, bluestem *(Andropogon* spp.) and panicum *(Panicum* spp.) grasses predominate; to the east, wiregrass (pineland threeawn, *Aristida stricta)* is most common.

With a reduction in fire occurrence, hardwoods and other pines encroach on the longleaf forest. Within the range of slash pine *(Pinus elliottii)*, this species becomes increasingly important, leading to the cover type Longleaf Pine–Slash Pine. Elsewhere loblolly and shortleaf pines *(P. taeda* and *P. echinata)* as well as hardwoods gradually replace the longleaf, eventually resulting in Loblolly Pine–Hardwood (Type 82) or occasionally Loblolly Pine–Shortleaf Pine (Type 80). On poor, dry sandhills and mountain ridges, scrub hardwoods invade the understory creating forest cover type Longleaf Pine–Scrub Oak and finally Southern Scrub Oak (Type 72) as the pine disappears *(12)*.

Hardwoods most closely associated with longleaf pine on mesic Coastal Plain sites include southern red, blackjack, and water oaks *(Quercus falcata, Q. marilandica,* and *Q. nigra)*; flowering dogwood *(Cornus florida)*; blackgum *(Nyssa sylvatica)*; sweetgum *(Liquidambar styraciflua)*; persimmon *(Diospyros virginiana)*; and sassafras *(Sassafras albidum)*. The more common shrubs include gallberry *(Ilex glabra)*, yaupon *(I. vomitoria)*, southern bayberry *(Myrica cerifera)*, shining sumac *(Rhus copallina)*, blueberry *(Vaccinium* spp.), huckleberry *(Gaylussacia* spp.), and blackberry *(Rubus* spp.). On xeric sandhill sites, the most common associates are turkey, bluejack, blackjack, sand post, and dwarf live oaks *(Quercus laevis, Q. incana, Q. marilandica, Q. stellata* var. *margaretta,* and *Q. minima)*. On the dry clay hills and mountains of Alabama, blackjack, post *(Q. stel-*

lata) and southern red oaks, and mockernut hickory *(Carya tomentosa)* are found with longleaf pine. On low, wet flatwood sites near the coast, the most conspicuous understory plants are gallberry and saw-palmetto *(Serenoa repens)*. Other common understory plants in low, wet Longleaf Pine or Longleaf Pine–Slash Pine types are sweetbay *(Magnolia virginiana)*, swamp cyrilla *(Cyrilla racemiflora)*, large gallberry *(Ilex coriacea)*, buckwheat-tree *(Cliftonia monophylla)*, blueberries, and blackberries.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Like all species in the pine family, longleaf pine is monoecious. The strobili of longleaf pine, both male (catkins) and female (conelets), are initiated during the growing season before buds emerge. Catkins may begin forming in July, while conelets are formed during a relatively short period of time in August. The number of flowers produced is apparently related to weather conditions during the year of initiation. A wet spring and early summer followed by a dry period in late summer promotes conelet production *(27)*. Catkin production, however, is favored by abundant rainfall throughout the growing season. Female strobili are borne most frequently in the upper crown, and male strobili predominate in the lower crown *(26)*. Late summer rainfall depresses conelet initiation, probably because vigorous exposed shoots in the middle and upper crown continue to grow. In the lower crown, where most catkins are borne, shoots stop growing earlier than they do in the upper crown.

Since rainfall patterns associated with catkin initiation differ from those favoring conelets, large crops of male and female flowers do not necessarily coincide. Ten years of observation did not show any correlation between size of conelet and pollen crops in longleaf pine.

Variable but usually heavy annual losses of longleaf pine conelets can be expected; observed losses have ranged from 65 to 100 percent *(2,24,30)*. Several agents, alone or in combination, may be responsible. The more important appear to be insects, bad weather, and insufficient pollen. Over 15 years at one location, cone production was related to pollen density, to the point of a sufficiency of pollen *(2)*. Further increases in pollen density had little effect. In some cases, nearly all the losses have been attributed to insects *(24)*, while in others the more common causes of conelet losses were not responsible *(30)*. Most conelet losses seem to occur in the spring, at about the time of pollination, although substantial losses may also occur in the summer *(24)*. Most of the spontaneous conelet abortions in longleaf pine may result from excess ethylene production by foliage and shoots. A foliar spray with antiethylene compounds soon after anthesis has reduced conelet abortion by half, doubling seed yields *(18)*.

Catkin buds normally emerge in November, then remain dormant for about a month before growth resumes. Conelet buds emerge in January or February. The rate of development of both conelets and catkins thereafter is almost entirely dependent on ambient temperature. Catkins are purple from the time they emerge from the buds until they shed their pollen. Upon emerging from the bud, conelets are red until they are pollinated, after which they gradually fade to a yellowish green. Most mature catkins range from 3 to 5 cm (1.2 to 2.0 in) in length.

The average date of peak pollen shed and conelet receptivity may range from late February in the southern part of longleaf pines' range to early April toward the northern limits. Most locations may experience flowering dates close to these extremes. The date of peak pollen shed and conelet receptivity coincides on individual longleaf pine trees but can vary considerably among trees in a stand. Some trees are consistently early and others late in time of flowering, although the differences vary from year to year, depending on air temperatures before and during the flowering period *(5)*. Over 22 years of observation, the time required for shedding 80 percent of all pollen in a longleaf pine stand ranged from 5 to 21 days and averaged 13 *(5)*.

Pollination takes place in the late winter or spring, but fertilization does not occur until the following spring. At this time conelets are growing rapidly, increasing in length from about 2.5 cm (1 in) in February to about 18 cm (7 in) by May or June *(16)*. Mature cones range in length from 10 to 25 cm (4 to 10 in). Cones reach maturity between mid-September and mid-October of their second year. Cones, as they become ripe, change color from green to dull brown, although cones may be ripe before the color change *(26)*. The specific gravity of ripe cones ranges from 0.80 to 0.89. Ripeness can be tested by flotation in SAE 20 motor oil; ripe cones will float but those not yet ripe will sink *(26)*.

Seed Production and Dissemination—Tree size, crown class, stand density, site quality, and, most important, genetic predisposition, all affect cone production by an individual tree. The best cone producers are dominant, open grown trees with large crowns, 38 cm (15 in) or more in d.b.h., with a past record of good cone production *(11)*. Trees 38 to 48 cm (15 to 19 in) in d.b.h. have produced an average of 65 cones annually compared to 15 cones by trees from 25 to 33 cm (10 to 13 in) in d.b.h. The number of sound seeds per cone varies widely and is related to size of seed crop in a particular year. In good seed years there may be about 50 seeds per cone, in average years 35, and in poor years 15 *(10)*.

Seed production per hectare reaches a peak at stand densities between 6.9 and 9.2 m^2/ha (30 to 40 ft^2/acre) of basal area, assuming that the stand is comprised of dominant-codominant trees of cone bearing size *(3)*. A shelterwood stand with a basal area of 6.9 m^2/ha (30 ft^2/acre) produces three times as many cones per unit area as a stand of scattered seed trees averaging 2.3 m^2/ha (10 ft^2/acre) in good seed years *(11)*.

Throughout its range, longleaf pine in shelterwood stands produces seed crops adequate for natural regeneration, about 2,500 cones per hectare (1,000/acre), on the average of once every 4 to 5 years *(11)*. However, everything else being equal, good cone crops are more frequent in some parts of the longleaf pine range than in others, so the general average may be meaningless at a given location. The production of female strobili is much less variable from place-to-place than is the produciton of mature cones, indicating that geographic differences in cone production are due more to conelet and cone losses than failure to produce conelets in the first place *(7)*.

When a shelterwood stand is created by cutting back a stand of substantially higher density, increased cone production resulting from release does not occur until the end of the third growing season after cutting *(9)*. Release that occurs after conelet initiation has no effect on that crop, other than promoting better conelet survival through reduced stress in dry periods.

Seeds are dispersed by the wind. Seed dispersal begins in late October and continues through November, with the majority falling within a period of 2 to 3 weeks. The time and duration of seed dispersal vary depending on weather conditions. Dispersal range is limited, with 71 percent of sound seeds falling within a distance of 20 m (66 ft) of the base of parent trees *(11)*.

Longleaf seeds are the largest of the southern pines. The number of cleaned seeds ranges from 6,600 to 15,400/kg (3,000 to 7,000/lb), averaging 10,800/kg (4,900/lb) *(26)*.

Seedling Development—Longleaf pine differs from other southern pines in that seeds germinate soon after they are dispersed. Given optimum conditions, seeds germinate in less than a week after they reach the ground. Prompt germination reduces the period of exposure to seed predators, but newly germinated seedlings are susceptible to damage or loss from animals, diseases, and weather uncertainties, which may include high fall temperatures, drought, or extreme cold with a risk of frost heaving in heavy soils *(11)*.

Seeds require contact with mineral soil for satisfactory germination and establishment. Longleaf seeds, with their large wings, cannot easily reach mineral soil through a heavy cover of grass and litter. The accumulated material must be removed before seedfall, either mechanically or by burning. Burning within a year of seedfall normally provides an adequate seedbed. Lack of seedbed preparation can result in a regeneration failure.

Germination of longleaf pine seed is epigeal *(26)*. Newly germinated seedlings have virtually no aboveground hypocotyl, and the cotyledons are close to the ground line. The primary needles appear after germination and the secondary needles about 2 months later. The epicotyl, or stem above the cotyledons, does not elongate rapidly as in most other pines. Even in the nursery, seedlings are virtually stemless after one growing season *(16)*. This stemless condition is one of the unique characteristics of longleaf pine. It is referred to as a grass stage and may last 2 to many years, depending on growth conditions. During this time, longleaf is most susceptible to its major disease, the brown-spot needle blight, *Scirrhia acicola (11)*.

While in the grass stage, seedlings develop extensive root systems. Growth can be followed by observing the increase in root-collar diameter. When it approaches 2.5 cm (1 in), active height growth is imminent. Grass-stage seedlings, once they reach 0.8 cm (0.3 in) in root-collar diameter, are highly resistant to fire, even during the growing season. Seedlings in early height growth, up to a height of about 0.6 to 0.9 m (2 to 3 ft), become susceptible to damage by fire. Once beyond this stage, longleaf pines are again fire resistant.

Competition and brown-spot needle blight have great impact on the rate of seedling development and together largely determine the duration of the grass stage. Longleaf seedlings can be easily established and usually survive for years under an overstory of parent pines. Growth, however, is very slow. Seedlings respond promptly with an increased rate of growth when released from overstory competition.

Growth rate varies widely among individuals in a natural seedling stand, and vigorous fast-growing seedlings express dominance early. The rapid breakup of a seedling stand into a wide range of size classes reduces the risk of stand stagnation (fig. 2). About 10 percent of a natural seedling stand shows resistance to the brown-spot disease, and this gives them a growth advantage that persists for many years. At age 24, trees that had little or no brown-spot infection averaged 2.4 m (8 ft) taller than trees that had 30 percent or more of their foliage destroyed by the disease as seedlings *(1)*.

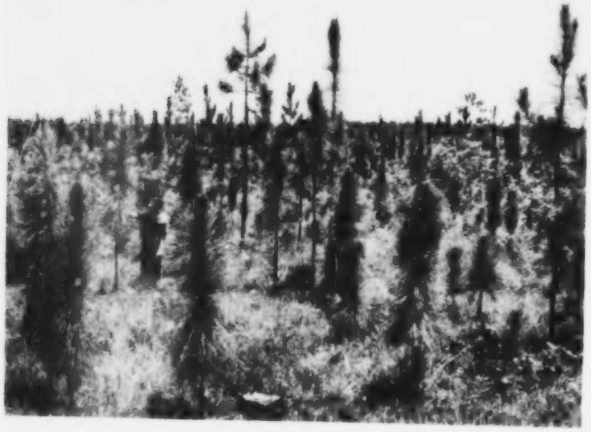

Figure 2—*Longleaf seedling and sapling stand 6 years after overstory removal. Despite range in sizes, nearly all trees are the same age.*

A low level of competition permits early initiation of height growth. One longleaf pine plantation on a prepared site had nearly 60 percent of the trees in active height growth by the end of the second growing season, and over 90 percent by the end of the third. Early initiation of height growth circumvented a brown-spot problem as the disease did not have time to build up to serious proportions.

Vegetative Reproduction—Longleaf pine seedlings, if top killed, can sprout from the root collar. Sprouting ability decreases sharply when seedlings begin height growth. In one study, almost 40 percent of seedlings cut off at the ground line during grass stage had living sprouts a year later. Only 14 percent of seedlings up to 1.37 m (4.5 ft) in height so treated developed sprouts, however, and those larger than this did not sprout at all *(14)*. Longleaf is not as easy to reproduce asexually as some of the other southern pines. Cuttings can be rooted but the process is difficult. Air-layering has met with limited success. Grafting has proven to be a reliable technique, and this is now the most common method of establishing seed orchards *(28)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Longleaf pine is a high quality timber tree, well suited to a whole range of products—poles, piling, posts, sawlogs, plywood, pulpwood, and naval stores. Longleaf naturally prunes itself well. Most stems are well formed, straight, and largely free of branches. The species almost always has higher stemwood specific gravities and produces more dry wood per unit volume than either loblolly or slash pine *(28)*. Intense exploitation since colonial days, plus lack of planned regeneration, contributed to the decline of longleaf pine forests that continues to this day. Once height growth has begun, the species can grow as well as the other major southern pines on many sites originally occupied by longleaf, and often exceeds them in growth.

The critical element in the growth of longleaf pine stands is the duration of the grass stage. About 70 percent of the variation among plantations in the form of height-over-age curves was related to the condition of the planting site: early height growth on unprepared cutover sites was much slower than on old fields and mechanically prepared cutover sites *(6)*.

Reduction of competing ground cover in grass stage seedling stands can have a large impact on growth and future volume yields. One study *(25)* observed the effects of a single aerial application of 2,4,5-T to stands of 1-year-old longleaf seedlings. Twenty years later, treated stands had significantly greater tree diameter (10 percent), height (17 percent), and total volume per unit area (32 percent) than adjacent untreated stands, although there was no difference in the number of trees per unit area. Treated stands averaged 83.5 m^3/ha (1,193 ft^3/acre) total inside-bark (i.b.) volume, compared to 63.2 m^3/ha (904 ft^3/acre) for untreated stands.

Longleaf pine growth and yield predictions have been published for periodically thinned even-aged natural stands *(15)* and also for unthinned plantations in the west Gulf region *(22)*. Predicted total volume (i.b.) yields for two common site index classes are given in table 1. The merchantable proportion of total volume ranges from 78 to 86 percent at age 20, to 97 to 98 percent at age 40. The peak in periodic annual increment is reached between ages 20 and 30.

The optimum stand density to maintain by periodic thinning varies by site and management goals. A rather broad range of stand densities, above a basal area of about 13.8 m^2/ha (60 ft^2/acre), produces near maximum periodic volume growth *(13)*. Lower densities concentrate growth on fewer trees. Longleaf responds well to release provided by thinning if the released trees have crowns equal to at least one-third

Table 1—Predicted total volume yields inside bark for even-aged natural stands of longleaf pine

Stand age in years[1]	Basal area	Site index at base age 50 years	
		21.3 m or 70 ft	24.4 m or 80 ft
	m²/ha	*m³/ha*	*m³/ha*
20	13.8	61	71
25	20.0	110	128
30	25.5	160	187
35	29.6	207	241
40	33.1	248	289
	ft²/acre	*ft³/acre*	*ft³/acre*
20	60	874	1,019
25	87	1,572	1,832
30	111	2,287	2,666
35	129	2,954	3,443
40	144	3,549	4,137

[1] Determined from ring counts taken at 1.2 m (4 ft), plus 7 years.

to one-half of total tree height. Small-crowned intermediate or suppressed trees do not respond promptly to release. Thinning should be from below to release well-formed dominant and codominant trees.

Present indications are that longleaf pine plantations should produce volume growth similar to natural stands if other factors are equal. To the extent that plantations have had better competition control, with consequent acceleration of early growth, a particular volume yield should be reached at an earlier age in plantations than in natural stands.

Rooting Habit—Longleaf pine develop massive taproots that, in mature trees, may extend to a depth of 2.4 to 3.7 m (8 to 12 ft) or more. A hardpan can arrest downward growth of the taproot. If the hardpan is close to the surface, windfirmness of the tree is reduced. Longleaf pines develop extensive lateral root systems. Most lateral roots are within 0.3 m (1 ft), and nearly all within 0.6 m (2 ft), of the surface *(29)*.

Reaction to Competition—Longleaf pine is intolerant of competition, whether for light or for moisture and nutrients. The species will grow best in the complete absence of all competition, including that from other members of the species. Fortunately, as noted earlier, young even-age longleaf pine stands break up rapidly into a broad range of size classes, due to variability in duration of the grass stage. Stagnation is almost never a problem. However, even suppressed trees in a stand will slow the growth of dominant neighbors. Optimum stand density for development of crop trees needs to be maintained by periodic thinning. Given release from neighboring trees, dominant and codominate trees in an overdense stand will respond promptly with increased diameter growth, as will some intermediate trees that retain crown ratios of 30 percent or more. Suppressed trees, while they may continue to live, rarely respond to release with improved growth.

Damaging Agents—Longleaf pine is less susceptible to most damaging agents than the other southern pines and is a relatively low risk species to manage. It is strongly resistant to fire, except as a small seedling of less than 0.8 cm (0.3 in) root collar diameter and in early height growth. It is also resistant to most pathogenic agents. The major disease is the brown-spot needle blight. This disease causes serious damage only to grass-stage seedlings. Continued severe defoliation by brown-spot suppresses and eventually destroys seedlings. Once rapid height growth begins, seedlings are no longer seriously afflicted. Seedlings growing in the open are most vulnerable, particularly if the groundcover is sparse; the disease usually does not seriously affect seedlings growing under a pine overstory. Other diseases occasionally of economic importance in local areas are pitch canker *(Fusarium moniliforme* var. *subglutinans)*, annosus root rot *(Heterobasidion annosum)* in thinned plantations, cone rust *(Cronartium strobilinum)* near the coast, and also the condition known as dry face of turpentined trees. Fusiform rust *(Cronartium quercuum* f. sp. *fusiforme)* is rarely a problem for longleaf pine *(20)*.

Many species of birds, mice, and squirrels feed on longleaf pine seeds, the latter often taking them from unripe cones. Several species of ants feed on germinating seeds and cotyledon seedlings. Cottontails as well as other predators can destroy newly established seedlings. Grass-stage seedlings are vulnerable to destruction by hogs, pales weevil *(Hylobius pales)*, and heavy livestock grazing. Pocket gophers cut seedlings off just below the ground surface.

Most seedling losses occur during the first year after establishment, untimely drought being the greatest single hazard. Logging of the overstory can destroy close to 50 percent of a seedling stand, although actual damage depends on type and season of logging, volume removed, and seedling size. Fire takes its toll of small, weak, or diseased seedlings.

Longleaf pine can be damaged by ice storms but is less susceptible to ice damage than slash pine *(19)*.

The southern pine beetle *(Dendroctonus frontalis)* does not seem to afflict the species severely. The black turpentine beetle *(Dendroctonus terebrans)* can be a problem, especially on trees injured by turpentining, logging, or fire. Perhaps the greatest single cause of mortality in longleaf stands of pole and sawlog size is lightning, which is often followed by infestation by bark beetles (*Ips* spp.). Windthrow from hurricanes or tornados can cause heavy losses locally. Long term observations throughout the longleaf region have shown an average annual mortality of 1 tree per hectare (0.4/acre) in mature longleaf pine stands *(4)*.

Special Uses

Longleaf pine is used for a broad range of forest products. Even old lightered stumps (those having resin-soaked heartwood characteristic of old trees) are pulled out and the stumpwood destructively distilled for chemicals. Longleaf "pine straw" is in demand for use as a mulch, so fresh needle litter is sometimes collected, baled, and sold. The longleaf pine forest, if regularly burned, has a parklike appearance with an understory dominated by grasses and forbs (fig. 3); an excellent habitat for game, especially quail, and quail hunting has long been associated with this timber type. The understory produces a substantial amount of high quality forage for both cattle and deer *(17,31)*. Mature longleaf stands also provide the most desirable habitat for the red-cockaded woodpecker.

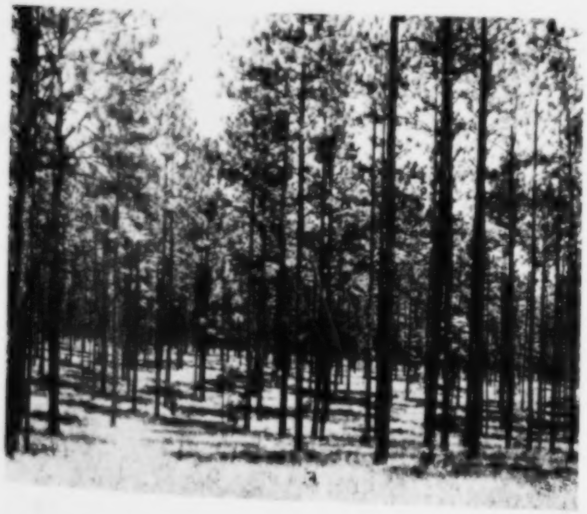

Figure 3—*Forty-five-year-old second-growth longleaf stand regularly burned. Note grass cover and scarcity of hardwoods and shrubs.*

Genetics

Population Differences

Longleaf pine is a highly variable species, and a considerable proportion of this variation is genetic. Considering the economically important traits, longleaf pines have as much or more genetic variation than other southern pines.

Variation among individual trees is greater than that among stands or among geographically diverse seed sources *(23,28)*. Nevertheless, the diversity of environments throughout the longleaf range has promoted the development of genetic variation among populations. According to rangewide provenance tests, trees from coastal areas usually outgrow those from inland areas at all but the coldest locations. Trees originating from the central Gulf Coast should be more productive than trees from other sources on most coastal plain longleaf sites from Georgia and north Florida west to east central Louisiana *(28)*. Elsewhere, local seed sources may be safest to use until more information is available.

Hybrids

The major southern pines, as well as some minor species, are closely related and have overlapping ranges. Natural hybridization has contributed to genetic diversity among trees and populations. Natural hybridization is common between longleaf and loblolly pine, producing the Sonderegger pine (*P.* × *sondereggeri* H. H. Chapm.). This is the only named southern pine hybrid. Throughout much of the longleaf pine range, the flowering of longleaf and loblolly pines overlaps in most years so there is no phenological barrier to natural crossing. Natural hybridization between longleaf and slash pine is unlikely, based on differences between the species in dormancy and heat requirements for flowering *(5)*.

Artificial crosses between longleaf pine and both loblolly and slash pines can be achieved easily. Crosses between longleaf and shortleaf pine have not been found in nature but have been produced artificially. There are no reported successful crosses of longleaf pine with any other pine species *(28)*.

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Pinus ponderosa Dougl. ex Laws. Ponderosa Pine

Pinaceae Pine family

William W. Oliver and Russell A. Ryker

Ponderosa pine *(Pinus ponderosa)*, also called western yellow pine, is one of the most widely distributed pines in western North America. A major source of timber, ponderosa pine forests are also important as wildlife habitat, for recreational use, and for esthetic values. Within its extensive range, two varieties of the species currently are recognized: *Pinus ponderosa* var. *ponderosa* (Pacific ponderosa pine) (typical) and var. *scopulorum* (Rocky Mountain ponderosa pine) *(10)*. Arizona pine *(P. arizonica)*, sometimes classified as a variety of ponderosa pine *(12,36,51)*, is presently recognized as a separate species *(45)*.

Habitat

Native Range

The range of ponderosa pine (fig 1) extends from southern Canada into Mexico, and from the Plains States of Nebraska and Oklahoma to the Pacific Coast.

Pacific ponderosa pine (var. *ponderosa*) ranges from latitude 52° N. in the Fraser River drainage of southern British Columbia, south through the mountains of Washington, Oregon, and California, to latitude 33° N. near San Diego. In the northeast part of its range it extends east of the Continental Divide to longitude 110° W. in Montana, and south to the Snake River Plain, in Idaho *(1,51)*.

Rocky Mountain ponderosa pine (var. *scopulorum*) extends east of the Continental Divide from latitude 48° N. in north-central Montana, southeasterly into North and South Dakota, eastern Wyoming, and as far east as north-central Nebraska. Within this area, ponderosa pine grows on the discontinuous mountains, plateaus, canyons, and breaks of the plains, with the most extensive stands found in the Black Hills of South Dakota and Wyoming *(51)*. South of Wyoming, Rocky Mountain ponderosa pine extends south on both sides of the Continental Divide, west to Arizona, and the eastern edge of the Great Basin in Nevada, east to Texas west of the Pecos River, New Mexico, extreme northwestern Oklahoma, Colorado, and northern Mexico *(36)*. Within this wide range, ponderosa pine is absent from a large area that includes southwestern Montana, western Wyoming, southern Idaho, and part of the Great Basin *(12,61)*. A possible explanation for the absence is that the distribution of rainfall during the summer months prevents seedling establishment except at higher elevations, where the species has little tolerance for the shorter growing season *(61)*.

Arizona pine (var. *arizonica*) is found primarily in the mountains of extreme southwestern New Mexico, southeastern Arizona, and northern Mexico *(36)*.

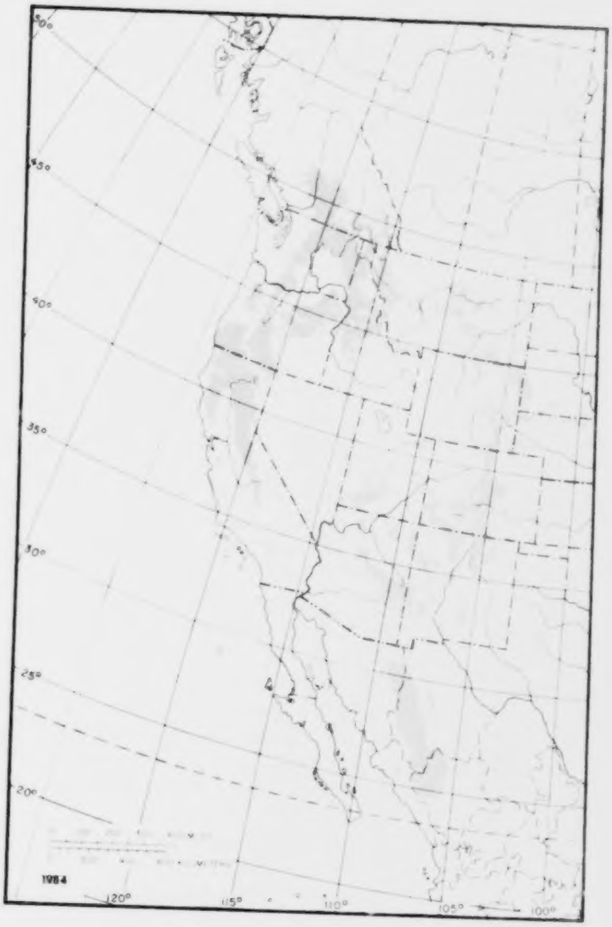

Figure 1—*The native range of ponderosa pine.*

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Climate

Throughout the range of ponderosa pine, soil moisture is the variable most often limiting growth, especially in summer when rainfall is deficient. For the east slope of the Rockies, the Black Hills, Utah, and the Southwest, however, summer rains occur, although the Southwest regularly experiences scanty May–June precipitation. In eastern Oregon and Washington, average annual precipitation ranges from 355 to 760 mm (14 to 30 in), much of it snow *(30)*. July, August, and September are dry; average rainfall is less than 25 mm (1 in). In Montana, east of the Continental Divide, average annual precipitation in ponderosa pine forests ranges from 280 to 430 mm (11 to 17 in), with 125 to 250 mm (5 to 10 in) received during the May-to-August period *(1)*. In the Black Hills of South Dakota, average annual precipitation is 410 to 710 mm (16 to 28 in), with up to 330 mm (13 in) received from May to August *(67)*. In northern Arizona, 150 mm (6 in) of the total growing season precipitation of 205 mm (8 in) occurs in July and August, after the May–June dry period. The west slope of the northern Sierra Nevada in California, where annual rainfall reaches 1750 mm (69 in), may be the wettest area supporting ponderosa pine in any quantity *(13)*.

The extent of the seasonal rainfall deficiency is evident from the July and August precipitation, usually about 25 mm (1 in) or less; in some places, as in California, July and August precipitation is often lacking. Except on coarse-textured soils, summer showers probably provide scant moisture useful to young seedlings. Total growing season precipitation may mean little because of the distribution pattern *(13)*.

Regardless of the location where ponderosa pine grows, average annual temperatures are between 5° and 10° C (41° and 50° F), and average July–August temperatures are between 17° and 21° C (62° and 70° F). Average frost-free seasons for ponderosa pine range from 90 to 154 days in eastern Montana and South Dakota *(1,63)* to more than 200 days in central California. Annual extremes are from -40° to 43° C (-40° to 110° F).

Soils and Topography

Ponderosa pine grows on soils derived from igneous, metamorphic, and sedimentary parent materials, including quartzite, argillite, schist, shale, basalt, andesite, granite, cinders, pumice, limestone, and sandstone. This results in a variety of soil orders including Entisols, Inceptisols, Mollisols, Alfisols, and Ultisols on which the species is found throughout its extensive range.

Its distribution on drier sites is related closely to supplies of available soil moisture which, in turn, are related to soil textures and depth *(13,20,22)*. In Wyoming, for instance, at the lower limits of coniferous forest, ponderosa pine is found only on coarse-textured soils of sandstone origin where the limited moisture is more readily available than on fine-textured soils of limestone origin *(27)*. In Oregon and Washington, higher survival and growth rates of ponderosa pine have been reported for coarse-textured sandy soils than for fine-textured clayey soils *(20)*.

Ponderosa pine stands, 51, 75, and 78 years old, growing in coarse-, medium-, and fine-textured soils in Montana, had their greatest root development in the medium-textured soils and the least in the fine-textured soils. Root concentration was more uniform in the medium-textured soils and concentration dropped off abruptly below a soil depth of 46 cm (18 in) in the fine-textured soils *(13)*.

Depending on the locality and the horizon of the samples, soils vary from pH 4.9 to pH 9.1. The pH in the surface horizon frequently is from 6.0 to 7.0 *(13)*.

Foliar concentrations of nitrogen and phosphorus needed for adequate growth are low in ponderosa pine compared with the associated conifers in California—Douglas-fir *(Pseudotsuga menziesii)*, white fir *(Abies concolor)*, sugar pine *(Pinus lambertiana)*, and incense-cedar *(Libocedrus decurrens)*. Foliar concentrations of 0.9 percent for nitrogen and 0.08 percent for phosphorus mark critical boundaries between nutrient deficiency and sufficiency *(42)*. Correcting nitrogen deficiency in California and central Oregon stands has increased volume growth 30 percent *(50)*. Because critical levels of foliar nitrogen and phosphorus are lower in ponderosa pine, while early biomass gains generally are greater, this species is judged superior in satisfying its nutritional needs on soils that by other species' standards are infertile.

Ponderosa pine is found at elevations from sea level to 3050 m (10,000 ft). From north to south the species grows at progressively higher altitudes and within more restricted elevational limits *(1,13,20,67)*. In Washington, the elevations for ponderosa pine are sea level to 1220 m (4,000 ft); in the Blue Mountains of northeastern Oregon, 910 to 1520 m (3,000 to 5,000 ft); in the south–central Oregon pumice area, 1460 to 2010 m (4,800 to 6,600 ft); in the northern Rocky Mountains, from 300 to 1830 m (1,000 to 6,000 ft); in the middle Rockies up to 2590 m (8,500 ft); and in the southern Rockies, up to 3050 m (10,000 ft). In

California, ponderosa pine is usually found at elevations from 150 to 1070 m (500 to 3,500 ft) in the north, and from 1610 to 2230 m (5,300 to 7,300 ft) in the south.

Associated Forest Cover

Ponderosa pine can be either a climax or a seral species *(18,27,47,61)*. It is a climax species at the lower limits of the coniferous forests, and a seral species in higher elevation mesic forests where more competitive conifers are capable of growing. In climax forests, ponderosa pine stands often contain many small, even-aged groups rather than a true uneven-aged structure.

Fires have had a profound effect on the distribution of ponderosa pine. Although the seedlings are readily killed by fire, larger trees possess thick bark, which offers effective protection from fire damage. Competing tree species, such as grand fir *(Abies grandis)* and Douglas-fir, are considerably less fire tolerant, especially in the sapling and pole size classes. Ponderosa pine, therefore, was able to maintain its position as a dominant seral species on large areas of middle-elevation forests in the West. Because of successful fire control during the past 50 years, many of these stands have developed understories of Douglas-fir and true firs. Type conversion has been accelerated by harvest of the ponderosa pine, leaving residual stands composed of true fir, Douglas-fir or lodgepole pine *(Pinus contorta* var. *latifolia) (15,20)*. In the Pacific Northwest, forest cover types on about 2 million ha (5 million acres) are believed to have changed in the last 25 years *(3)*.

Ponderosa pine is an integral component of three forest cover types in the West: Interior Ponderosa Pine (Society of American Foresters Type 237), Pacific Ponderosa Pine–Douglas-Fir (Type 244), and Pacific Ponderosa Pine (Type 245) *(18)*. Interior Ponderosa Pine is the most widespread type, covering most of the range of the species from Canada to Mexico, and from the Plains States to the Sierra Nevada, and the east side of the Cascade Mountains. Ponderosa pine is also a component of 65 percent of all western forest cover types south of the boreal forest.

Major associated tree species are as follows:

Northwest. Rocky Mountain Douglas-fir *(Pseudotsuga menziesii* var. *glauca)*, lodgepole pine, grand fir, and western larch *(Larix occidentalis)*.

California. California white fir *(Abies concolor* var. *lowiana)*, incense-cedar, Jeffrey pine *(Pinus jeffreyi)*, sugar pine, coast Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)*, California black oak *(Quercus kelloggii)*, and western juniper *(Juniperus occidentalis)*.

Rocky Mountains and Utah. Rocky Mountain Douglas-fir, blue spruce *(Picea pungens)*, lodgepole pine, limber pine *(Pinus flexilis)*, and quaking aspen *(Populus tremuloides)*.

Black Hills. Quaking aspen, white spruce *(Picea glauca)*, and paper birch *(Betula papyrifera)*.

Arizona and New Mexico. White fir *(Abies concolor* var. *concolor)*, Rocky Mountain Douglas-fir, blue spruce, quaking aspen, Gambel oak *(Quercus gambelli)*, and southwestern white pine *(Pinus strobiformis)* at higher elevations; Rocky Mountain juniper *(Juniperus scopulorum)*, alligator juniper *(J. deppeana)*, and Utah juniper *(J. osteosperma)* at lower elevations.

Genera of understory vegetation frequently found in ponderosa pine forests are as follows:

Shrubs. Arctostaphylos, Ceanothus, Purshia, Artemisia, Quercus, Rosa, Prunus, Spiraea, Symphoricarpos, Physocarpus, and *Berberis*.

Grasses. Agropyron, Andropogon, Bouteloua, Festuca, Muhlenbergia, and *Poa*.

Community composition varies widely with geographic location, soils, elevation, aspect, and successional status. Specific information is available in descriptions of various habitat and community type classifications *(1,20,23,27,35,47,61,63)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Ponderosa pine is monoecious. At pollination the male strobili, borne in short, dense clusters, are 2 to 3 cm (0.8 to 1.2 in) long and female conelets are 2.5 cm (1 in) long. In western Montana, central Idaho, and eastern Oregon, at elevations from 910 to 1830 m (3,000 to 6,000 ft), flowering generally begins between May 1 and 10. Pollen is shed May 25 to June 15, cones reach a full size of 8 to 15 cm (3 to 6 in) July 20 to August 10 of the next year, seed is ripe August 20 to September 5, cones begin to open September 1 to 13, and seed is shed until November. On the east and west sides of the Sierra Nevada in California, at an elevation of 1830 m (6,000 ft), however, cones develop about 2 weeks later *(13)*. In northern Arizona, near Flagstaff, pollen is shed between June 10 and 20 *(55)*, but at an elevation of 910 m (3,000 ft) on the west slope of California's Sierra Nevada, pollen has been collected as early as April 15; May 11 was average for a 7-year period. Also on the west slope of the Sierra Nevada, pollen is shed an average of 8 days later for each 300 m (1,000 ft) rise in elevation *(13)*.

In Colorado, at 2710-m (8,900-ft) elevation, during a 9-year period, female conelets emerged on or about

June 18 and only about 36 percent of them survived until the beginning of the second year. Flowering is correlated closely with the passing of freezing weather *(13)*.

Seed Production and Dissemination—No regular periodicity has been observed in the seed production of ponderosa pine over its entire range. In California, west of the Sierra Nevada, medium seed crops are borne on an average of every 2 to 3 years. The average interval between heavy cone crops is 8 years. Good cone crops are produced every 3 years in the Black Hills *(7)*, every 3 to 4 years in the Southwest *(55)*, and every 4 to 5 years in the Pacific Northwest *(3)*. Observations over 23 years in Montana show ponderosa pine to be a poor seeder west, and a fair seeder east, of the Continental Divide, with only one good crop. The species bears cones as early as 7 years and continues to produce good seeds to at least 350 years. Seeds from trees aged 60 to 160, however, are more viable than those of younger or older trees. In California, trees more than 64 cm (25 in) in d.b.h. were the best producers. In central Idaho, mature and overmature trees growing at an elevation of 1680 m (5,500 ft) produced lower quality seeds than similar trees at 1220 m (4,000 ft), and open grown trees produced heavier crops of larger cones than stand grown trees *(13)*.

In eastern Washington, Idaho, and western Montana, 16 species of insects have been identified as causing seed losses of ponderosa pine *(14)*. They destroyed up to 95 percent of the cone crop, but most areas sampled suffered losses ranging from 30 to 60 percent. In central Arizona, abortion, ponderosa pine cone beetles *(Conophthorus ponderosae)*, and ponderosa pine coneworms *(Dioryctria* sp.) were the three most important causes of cone mortality *(57)*. Usually the proportion of seeds lost to insects is highest when crops are small.

Ponderosa pine seeds are consumed by a great many birds and small mammals such as mice, chipmunks, and tree squirrels. In years of low cone production, the potential seed crop may be severely reduced. Squirrels clip many of the cone bearing twigs, destroying flowers and conelets *(13)*.

Specific gravity of cones containing ripe seed can be predicted. Cone collectors should consult local authorities before picking, however, because specific gravity of ripe cones varies from 0.80 in Arizona to 1.00 in the Black Hills.

The number of seeds per cone varies greatly among regions and ranges from only 31 seeds in northern Arizona *(55)* to 70 in central California *(13)*. Weight of cleaned seeds varies from 15,200 to 50,700/kg (6,900 to 23,000/lb) and averages 26,500/kg (12,000/lb) *(31)*.

Ponderosa pine seeds are not disseminated naturally over extensive distances. In central Oregon, seedfall at 37 m (120 ft) was only 22 percent of the seedfall at the west edge of a cleared area, and at 120 m (396 ft) it was only 8 percent *(3)*. Nearly all seeds are disseminated by early November. In a good seed year as many as 852,050 seeds per hectare (345,080/acre) may reach the ground *(19)*.

Seedling Development—Throughout ponderosa pine's range, except in the Black Hills and the west side of the Sierra Nevada, natural regeneration is sporadic. Successful natural regeneration is thought to be the result of the chance combination of a heavy seed crop and favorable weather during the next growing season. Soil texture, plant competition, and seedbed conditions are other common determinants of survival of young seedlings *(13)*.

Germination of ponderosa pine is epigeal *(31)*. Moisture stress reduces seed germination as well as initial seedling survival and growth. In an Arizona study, seed germination, root penetration, root dry weight, and cotyledon length decreased as the stress increased beyond 0.7 MPa (7 bars) *(55)*. Older seedlings, however, are able to cope with limited moisture supplies by reducing transpiration and by vigorously extending their root systems. Transpiration rate declines at soil water potentials of –0.1 to –0.2 MPa (–1 to –2 bars). At –1.0 MPa (–10 bars) the transpiration rate is only 12 percent of maximum *(37)*. Ponderosa pine has the capacity for root growth in relatively dry soil. Nursery stock lifted in January in California had appreciable root elongation even when planted in soil with a water potential of less than –0.9 MPa (–9 bars) *(62)* and has survived, at least for short periods, water potentials of less than –8.0 MPa (–80 bars) in the Southwest *(24)*.

The significance of competing vegetation as a deterrent to early survival and development of young seedlings has been clearly demonstrated. In central Idaho, soil moisture remained above the wilting point at depths below 15 cm (6 in) on areas free of competing vegetation throughout the growing season but dropped to or below that critical point on most vegetated plots *(13)*. In loamy soils in the White Mountains in Arizona, drought is normally not a major variable in seedling survival beyond age 2, except where there is grass cover *(30)*. Shrub competition reduced the height and diameter growth of ponderosa pine planted in northern California *(43)*; similar growth reductions have been reported for stands in Oregon *(4)*.

Air and soil temperatures often affect growth. Seedlings grown from seed collected in Arizona, California, and South Dakota had the best root growth in 15° C (59° F) air temperature and 23° C (73° F) soil temperature. Height growth was greatest at 23° C (73° F) temperature for air and soil *(33)*.

On the western slopes of the Sierra Nevada, height growth of ponderosa pine started significantly later with each increase of 610 m (2,000 ft) in elevation, and the length of the growing season was significantly shorter with a 910 m (3,000 ft) increase in elevation. Rates of height and radial growth did not vary with elevation during the period of growth. At an elevation of 1520 m (5,000 ft), a 6-year average showed that ponderosa pine started radial growth on March 23 and height growth on April 26. The period of radial growth lasted 177 days; that of height growth, 97 days. Ponderosa pine started height growth before sugar pine, incense-cedar, and white fir, but not before lodgepole pine *(13)*.

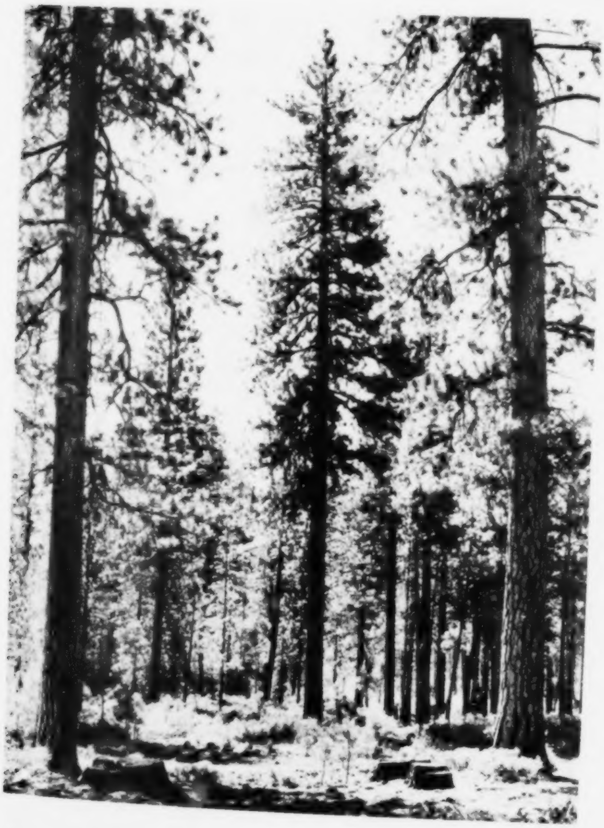

Figure 2—*A ponderosa pine stand.*

Many variables cause seedling mortality. Ponderosa pine seedlings less than 36 days old were more susceptible to minimum night temperatures (lower than –5° C (23° F)) than were lodgepole pine seedlings. But by 2 months of age, differences in tolerance did not exist *(8)*. During winters with little snow cover, 1- and 2-year-old seedlings suffered damage and killing from frost. In the Southwest, natural regeneration on fine-texured soils is almost non-existent because of frost-heaving *(24)*. Damage is lessened by heavy cover and early summer germination of seeds, which gives a longer establishment period. Ordinarily, older seedlings are hardy in severe winter temperatures, but occasionally they suffer "winter killing" of foliage (a desiccation process) if the temperature drops suddenly when drying winds and frozen ground are present. Also, 1- to 3-month-old seedlings are killed by stem temperatures of about 54° C (130° F) and higher. Ponderosa pine is more successful in resisting high soil surface temperature with increasing age; 110-day-old seedlings can successfully withstand instantaneous temperatures of 58° to 82° C (136° to 180° F) *(13)*. Also, it can withstand higher temperatures than its associates in the Northwest—Douglas-fir, grand fir, and Engelmann spruce *(Picea engelmannii) (56)*.

Vegetative Reproduction—Ponderosa pine does not reproduce naturally by vegetative methods. It can be propagated by rooting and grafting, but success decreases rapidly when scions are taken from trees older than 5 years *(64)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Ponderosa pine (fig. 2) grows to impressive size. Stems 263 cm (103.5 in) in d.b.h. and 70.7 m (232 ft) in height have been recorded *(13)*. Diameters at breast height of 76 to 127 cm (30 to 50 in) and heights of 27.4 to 39.6 m (90 to 130 ft) are common throughout most of its range. Trees often reach ages of 300 to 600 years.

Diameter growth can be rapid and remain fairly constant for long periods provided trees are given adequate growing space. In California, on productive sites, free-growing trees can reach 66 cm (26 in) in d.b.h. in 30 years or 22 cm (8.7 in) per decade (data on file at Pacific Southwest Forest and Range Experiment Station, Redding, CA). In central Oregon, where sites are less productive, trees 13 to 51 cm (5 to 20 in) in d.b.h. and from 19 to 36 years old can grow 12 cm (4.9 in) in d.b.h. per decade if free of intertree competition *(3)*. Trees in a virgin stand in Arizona grew 29 mm (1.14 in) on the average during

Table 1—Total bole volume inside bark of ponderosa pine 1.5 cm (0.6 in) and larger in d.b.h. *(39)*

Age	Site index at base age 100 years[1]			
	18 m or 60 ft	27 m or 90 ft	37 m or 120 ft	46 m or 150 ft
yr		*m^3/ha*		
20	28	94	168	262
40	122	238	396	588
60	192	340	570	861
80	238	413	696	1060
100	273	472	794	1204
120	308	518	868	—
140	336	556	928	—
yr		*ft^3/acre*		
20	400	1,350	2,400	3,750
40	1,750	3,400	5,650	8,400
60	2,750	4,850	8,150	12,300
80	3,400	5,900	9,950	15,150
100	3,900	6,750	11,350	17,200
120	4,400	7,400	12,400	—
140	4,800	7,950	13,250	—

[1] Height of dominant and codominant trees of average d b h

a 10-year period, but trees in a cutover stand grew 43 mm (1.68 in) *(55)*.

Vegetative competition can restrict diameter growth markedly whether it be from neighboring trees or understory shrubs. In the central Oregon study, trees completely surrounded by understory shrubs grew only 9 cm (3.5 in) per decade. Those trees with no competitive ground cover averaged 12 cm (4.7 in) of growth per decade. In California on a droughty, skeletal soil, severe shrub competition reduced diameter growth to less than half that of competition-free trees. Insect damage, which was greater on the trees competing with shrubs, accounted for some of the growth depression *(44)*. Stagnation in diameter, and often in height, represents a serious problem in densely stocked stands throughout the species' range, but especially on poor sites.

Height growth is most rapid in the pole and young sawtimber size classes to about 60 years. In the Pacific Northwest, dominant trees in stands of moderate density grow from 0.24 to 0.46 m (0.8 to 1.5 ft) annually between the ages of 20 to 60 years on timber-producing sites *(2)*. Rate of growth declines gradually at older ages. Arizona trees of 160 years or older (determined at breast height) grow little in height *(55)*. Height growth increases with site productivity and is more sensitive to stand density than was once believed.

Representative yields of ponderosa pine from a normal yield table for sites of various productivities are given in table 1 *(39)*. For extensive natural stands, table values should be reduced by 25 percent or more because of roads, rock outcrops, steep slopes, openings, and other unproductive areas.

Old-growth ponderosa pine produces clear, high-grade lumber, but young trees typically are limby. Natural pruning develops slowly. An average clear length of only 3.5 m (11.5 ft) was recorded in 250-year-old stands in central Idaho *(13)*.

Rooting Habit—The ability of ponderosa pine seedlings to grow vigorous taproots is one reason for their tenacity on severe sites where associated species often fail. Within a few months of germination, roots can penetrate to depths of 50 cm (20 in) or more in loosened and watered soil *(32)*. This rapid root growth is essential to ponderosa pine's apparent adaptation to the climate of the Southwest. There, seeds do not germinate until the soil is continuously warm and moist. These conditions are not present until summer rains begin, usually in July. Root growth was uninhibited by grass as long as moisture was abundant *(34)*. Taproots penetrate to about half that depth or less under average conditions in the field. Annually, for the next 2 years, lateral roots may double or triple in length.

Mature ponderosa pines put down a root to depths of more than 2 m (6 ft) in porous soils, but seldom more than 1 m (3 ft) in heavy clay soils. Exceptions occur in soils underlain by rock with deep fissures, where roots have been observed along cut banks at depths of 11 to 12 m (35 to 40 ft). In open stands, lateral roots may extend 46 m (150 ft). In dense stands, however, they are limited more to the crown width. The main mass of roots is concentrated within the top 60 cm (24 in) of the soil mantle.

Reaction to Competition—In the Sierra Nevada mixed conifer type in California, growth of advance regeneration of ponderosa pine was compared to that of associates beneath various overstory stand densities (data on file at Pacific Southwest Forest and Range Experiment Station, Redding, CA). Even beneath a light overstory stand casting 47 percent shade, ponderosa pine saplings grew only about half as rapidly as their associates (Douglas-fir, sugar pine, white fir, and incense-cedar) and about half of that expected for fully lighted pines. Relative to associates elsewhere within its range, ponderosa pine is more shade tolerant than western larch but less tolerant than grand fir and western white pine *(40)*. Overall, it is most accurately classed as intolerant of shade.

Because of ponderosa pine's intolerance of shade, it tends to grow in even-aged stands and is usually managed by that method. Uneven-aged stands might appear common throughout the drier portion of its range but are in reality a mosaic of even-aged groups. Ponderosa pines lose vigor in dense stands. On drier sites in the Pacific Northwest, trees in pole-size stands with basal area stand densities above 34.4 m^2/ha (150 ft^2/acre) become subject to attack by bark beetles *(54)*.

Ponderosa pine remains physiologically young and responds to release up to age 200 in Arizona. Elsewhere, stagnated sapling stands 70 to 100 years old usually respond to thinning and seem to grow as rapidly as unstagnated trees, when crowns grow to sufficient size to take advantage of the additional growing space *(3,7)*.

Damaging Agents—Rabbits and hares injure or kill many seedlings, and pocket gophers are especially destructive. In areas where pocket gopher populations are high all seedlings and many saplings may be destroyed. Squirrels and porcupines attack sapling and pole-size trees and, although rarely killing them, deform the stems on which they feed. Repeated browsing by deer has stunted seedlings for 50 years or more *(13,55)*. In the absence of regulation, sheep and cattle have damaged reproduction by trampling, bedding, and occasional browsing *(13)*.

At least 108 species of insects attack *P. ponderosa* var. *ponderosa*, and 59 species attack *P. ponderosa* var. *scopulorum (13)*. The most damaging of the tree-killing insects are several species of *Dendroctonus*. Trees die from the combined effects of a blue stain fungus transmitted by the beetle and extensive larval consumption of the phloem. The western pine beetle *(D. brevicomis)* is a common cause of mortality in overmature, decadent trees within the range of ponderosa pine from Baja California, north into Oregon, Washington, western Canada, Idaho, and western Montana. During epidemics, however, apparently healthy, vigorous trees are also killed. During the drought years of the 1930's, losses from western pine beetle in the Pacific Northwest were so heavy that many foresters feared for the pine stands' continued existence. The mountain pine beetle *(D. ponderosae)* is the most destructive and aggressive enemy in the central and southern Rocky Mountains. During the 1894–1908 outbreak in the Black Hills of South Dakota, this insect killed between 5.7 and 11 million m^3 (1 and 2 billion/fbm) of ponderosa pine *(13)*. Tree killing by *D. ponderosae* has increased with the conversion of old-growth to young-growth stands in the Pacific Northwest. High stand density is believed to reduce vigor of some of the larger trees in a stand and, therefore, is an underlying factor in the occurrence of bark beetle outbreaks. *D. adjunctus, D. approximatus*, and *D. valens* are other species of the genus that often kill ponderosa pines.

Among bark beetles, *Ips* species are second in destructiveness only to *Dendroctonus (21)*. *Ips* are present naturally in all stands, where they usually breed in slash. In abundant slash from forestry activities, *Ips* can kill vigorous ponderosa pine up to 66 cm (26 in) in d.b.h. when populations reach explosive levels. Eleven species of *Ips* have been found attacking ponderosa pine. Of these, *I. latidens, I. emarginatus, I. pini, I. lecontei*, and *I. paraconfusus* have the most impact.

Several insects mine buds and shoots, primarily of young trees. Although seldom killed, trees are retarded in growth when infestations are severe. Pine tip moths *(Rhyacionia* spp.) and the gouty pitch midge *(Cecidomyia piniinopis)* kill the buds and shoots they mine. A more insidious pest, until recently overlooked and overrated, is the western pineshoot borer *(Eucosma sonomana) (21)*. Larvae of this species bore within the pith of the terminal shoot, stunting but seldom killing them. Shoots that are potentially more robust are more likely to be infested than are weaker shoots. Accordingly, direct comparisons of infested vs. uninfested shoot lengths will underestimate actual growth loss. Each terminal shoot infested by a larva that developed to maturity was reduced in length that year by more than 25 percent in one study *(59)*.

The pine reproduction weevil *(Cylindrocopturus eatoni)*, a native of California and, presumably, Oregon, can be a threat to slow-growing plantations. Its impact has declined, however, with the improvement in planting stock and control of competing vegetation.

Defoliating insects, such as the pine butterfly *(Neophasia menapia)* and the pandora moth *(Coloradia pandora)*, periodically cause damage over extensive areas. The pine needle sheathminer *(Zelleria haimbachi)* can be locally severe in young stands.

Dwarf mistletoe *(Arceuthobium vaginatum* ssp. *vaginatum* in the Southwest, and *A. campylopodium* in California and the Northwest) is ponderosa pine's most widespread disease, absent only in the Black Hills *(25)*. It seems to be particularly devastating in the Southwest, where it infects trees on about one-third of the commercial acreage. At Fort Valley Experimental Forest in northern Arizona, dwarf mistletoe has caused up to 36 percent of the mortality *(55)*. On trees not killed, the parasite is responsible for a significant loss in growth, primarily in height, and is reported to reduce seed viability as much as 20 percent. In the Northwest, *A. campylopodium* has little effect on vigorous, young trees because height growth will usually exceed its upward spread, relegating the parasite to the lower crown *(5)*.

Several diseases attack ponderosa pine roots. Black stain root disease *[Leptographium* (syn. *Verticicladiella) wageneri]* causes a diffuse dark staining of the root wood and kills roots *(6)*. *Heterobasidion annosum* causes an insidious lethal root disease that is spread by airborne spores to the surfaces of freshly-cut stumps. It and *L. wageneri* kill trees of all ages and usually result in group mortality that is sometimes mistaken for the work of bark beetles, which are frequently secondary invaders. *Armillaria* sp., previously considered weak root and butt decayers, are causing increased mortality in young plantations and thinned stands where the disease can build up in dead root systems *(3)*. Active infection centers of *L. wageneri* and *H. annosum* spread about 1 m (3 ft) per year. The rate is usually less for *Armillaria* sp.

The most damaging heart rot in the southern Rocky Mountains and the Black Hills is western red rot caused by *Dichomitus squalens (25)*. It is a major cause of loss of sound wood in commercial stands. Because ponderosa pines older than 100 years have substantially greater defect, shorter rotation ages should eliminate much of the heart rot. *Phellinus pini* is the major heart rot in the Pacific Coast States.

A needle cast, *Elytroderma deformans*, found throughout ponderosa pine's wide range, is the most serious foliage disease *(6)*. It is unique among the needle casts in being perennial and in its capacity to infect the host twigs, which enables it to maintain its populations even under adverse environmental conditions. Although less destructive than the alarming appearance of affected trees suggests, it can slow growth and kill trees of sawtimber size. Bark beetles are prompt to attack infected trees. Severe damage from *E. deformans* was reported on the Ochoco National Forest in Oregon, where 555,900 m^3 (98,148,000 fbm) of dying and dead trees were removed from 1946 to 1950 *(13)*.

Several rusts of the *Cronartium coleosporioides* complex are damaging to ponderosa pine. Locally, especially in the Southwest, limb rust *(Peridermium filamentosum)* attacks middle or upper crowns of mature trees, killing branches in both directions as it spreads *(46)*. The western gall rust *(Endocronartium harknessii)* attacks ponderosa pine from the Black Hills to the Pacific Northwest *(25)*. It infects all ages, resulting in round and pear-shaped galls, distortions, and trunk lesions. Young trees may be killed. Comandra blister rust *(Cronartium comandrae)* is found in all states west of the Rocky Mountains but is most common in California, Idaho, Montana, Utah, and Wyoming. It causes scattered mortality in well-stocked sapling and small pole stands. In thinned stands, however, the disease may cause substantial damage *(3)*.

Air pollution is an increasing and vexing source of foliar damage to ponderosa pine. Ozone is the major plant-damaging constituent of photochemical oxidant air pollution. Ozone becomes concentrated enough to cause damage near the border of air basins and in the predominant summer downwind direction from heavily populated areas. Because ponderosa pine, especially var. *ponderosa*, is susceptible, and because it grows near areas heavily polluted, ozone damage can be great. Typical injury is a chlorotic mottling accompanied by premature abscission of old needles *(6)*. Moderately or severely injured trees are attacked more frequently by bark beetles and *Heterobasidion annosum* root disease *(28)*.

Basal fire scars are common on the thick-barked stems in old-growth ponderosa pine forests. Uncontrolled fire was common before European colonization. These surface fires consumed branches, fallen trees; understory vegetation, and some living trees. The fires burned from 1 to 47 years apart, with most at 5- to 20-year intervals *(3)*. Low-intensity fires kept many pine forests open and parklike. They also helped to maintain ponderosa pine in areas where more tolerant climax species would have attained dominance, because saplings or larger-sized ponderosa pine are more fire resistant than many of the true firs and Douglas-fir.

Survival and growth of ponderosa pine usually are affected little if 50 percent or less of the crown is scorched in a fire. Six years after a fire in Arizona, however, no poles and only 5 percent of the sawtimber-size trees were living if more than 60 percent of the crown had been destroyed *(13)*. Low tree vigor and cambium damage increase the likelihood of mortality. Vigorous young trees have survived, on occasion, when 100 percent of their crowns were scorched. Because buds are protected by thin long scales, late season fires cause less mortality. Continued accumulation of food reserves after diameter growth ceases in late summer also increases the ability of the tree to withstand fire injury. When crowns are scorched, young, fast-growing trees on good sites have the best chance of survival and old, slow-growing trees on poor sites the poorest chance.

Snow often injures saplings and larger trees. Stem bending and breaking from unusually wet snowfalls that overload tree crowns can seriously damage dense pole-size stands *(49)*. Stem deformation by snow pressure and movement on mountain slopes is a threat to sapling stands *(38)*, especially where ponderosa pine is planted above its optimum elevational limit.

Special Uses

In ponderosa pine forests, timber production, livestock grazing, and recreation are the principal land uses. Ponderosa pine forests are found at low elevations offering year-round recreation, and they frequently border forest highways where esthetic values are high. They provide habitats for various wildlife species. Abert's and Kaibab squirrels usually live in the ponderosa pine forests *(55)*. Snags in the mature pine forest provide a large number of species with nesting and roosting sites. Big game, such as deer and elk, also use the pine forests for food and shelter.

Genetics

Population Differences

Ponderosa pine shows distinct geographic variations over its widespread range. Within and between var. *ponderosa* and var. *scopulorum*, provenance studies *(51,65,66)* have shown genetic variation in growth, stem form, needle length, survival, initiation of leader growth, seasonal pattern of root growth potential, ability to germinate under moisture stress *(41)*, biotic and abiotic damage *(17,26,52)*, monoterpene production *(58)*, nutrient status *(29,68)*, and isozymes *(10)*. This wealth of information on genetic diversity was summarized and interpreted recently *(10)*. It suggests that var. *ponderosa* consists of three major geographic races and var. *scopulorum* of two major geographic races. Within var. *ponderosa*, the Pacific race is found in California northward from the Transverse Ranges and west of the Sierra Nevada and Cascade Range into northern Oregon. Pacific race pines have relatively large needles, cones, and seeds, and are rapid growing and least cold hardy in tests to date. The North Plateau race extends northward along the eastside of the Sierra Nevada and Cascade Range and east to the Continental Divide in Montana. Like the Pacific race, it has open, plume-like foliage, 3-needle fascicles and isozyme characteristics. But the North Plateau race has needles with thickened layers of hypoderm and sunken stomata, and is indistinguishable from the Rocky Mountain race in monoterpene characteristics. Least well understood, but distinct in monoterpene production, is the Southern California race.

Within var. *scopulorum*, the Rocky Mountain race comprises the northeast portion of the species' range. It is characterized by compact foliage, 2-needle fascicles, and better growth in trials east of its natural range. The Rocky Mountain race joins the Southwestern race along a broad, ill-defined front through southern Colorado, Utah, and Nevada. The Southwestern race has relatively open foliage, low proportions of 2-needle fascicles, and resins with distinctive monoterpene composition.

Results from a provenance study of 45-year-old trees in northern Idaho and a study of 30-year-old trees in Oregon and Washington *(60)* showed that 36 percent of the variation in the height of the trees was associated with seed source. A clinal variation was evident in the increase of height from sources in an east-to-west direction. This variation was related to September-through-June precipitation. Clinal variation in a latitudinal and altitudinal direction was related to April–May temperatures. Incidence of animal damage and of frost injury was related, also, to seed source.

Ponderosa pine varies markedly in its resistance to cold. In a test of 298 individual tree progenies planted in Michigan, all 2-year-old seedlings of California origin suffered severe injury from cold *(66)*. Progenies from British Columbia, Washington, eastern Oregon, Arizona, and southern New Mexico suffered light damage. No damage was reported for progenies from the remainder of the species' range. Essentially the same pattern was found in the northern Idaho study in 10- to 15-year-old trees *(65)*.

Elevational variation has been studied intensively in central Idaho *(53)* and in California *(9)*. On the west slope of the Sierra Nevada in California, seeds collected from trees growing at elevations of 40 to 2130 m (125 to 7,000 ft) were planted at altitudes of 290, 830, and 1720 m (950, 2,730, and 5,650 ft) above sea level. The general trend was that early growth was most rapid for mid-elevation sources and least rapid for high-elevation sources, regardless of the elevation of the plantation. But by 29 years, at the high-elevation plantation, sources from high elevations had overtaken sources from low elevations and had nearly caught up to sources from middle elevations. Middle and low elevation sources, especially the latter, suffered stem and leader damage from snow and wind, which significantly reduced their growth superiority. Wood specific gravity decreased with increasing elevation of parent source regardless of where the source was planted *(16)*. No elevational effect was discerned in tracheid length, although individual differences were found. Differences were recognized, also, in total height and diameter, and in the seasonal growth pattern *(42)* for families within elevational zones. Genetic diversity among populations, both in California and central Idaho, was readily interpretable as adaptive variation. Results of both studies suggest that for selective breeding of a wide-ranging species with distinct elevational differentiation, such as ponderosa pine, superior progenies can be obtained from selection within the optimum elevational zone of best geographic sources. In central Idaho, the recommended elevational zone is ± 180 m (600 ft).

Hybrids

Natural crosses of ponderosa pine with Jeffrey pine have been observed in California where their ranges overlap, but they are rare. Where the two species grow in the same stand, different flowering times and other reproductive barriers restrict crossing *(11)*. Ponderosa pine crosses with *Pinus montezumae* and *P. arizonica*, and rarely with *P. engelmannii (45)*. Introgressive hybridization has been observed with *P. washoensis*.

In addition to the natural hybrids, artificial crosses have been obtained with a number of other hard pine species, including *P. durangensis*.

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Pinus pungens Lamb. Table Mountain Pine

Pinaceae Pine family

Lino Della-Bianca

Table Mountain pine *(Pinus pungens)* is also called hickory pine, mountain pine, or prickly pine. It is most often small in stature, poor in form, and exceedingly limby. One large tree near Covington, VA, measures 70 cm (28 in) in d.b.h. and 29.6 m (97 ft) tall and has a crown spread of 10.4 m (34 ft). These pines are used locally for fuel and commercially for pulpwood, and they provide valuable watershed protection.

Habitat

Native Range

Table Mountain pine (fig. 1), an Appalachian endemic, grows almost entirely within the range of pitch pine *(Pinus rigida)* and Virginia pine *(P. virginiana)*, but is less frequent. In general, Table Mountain pine occupies xeric sites of Appalachian

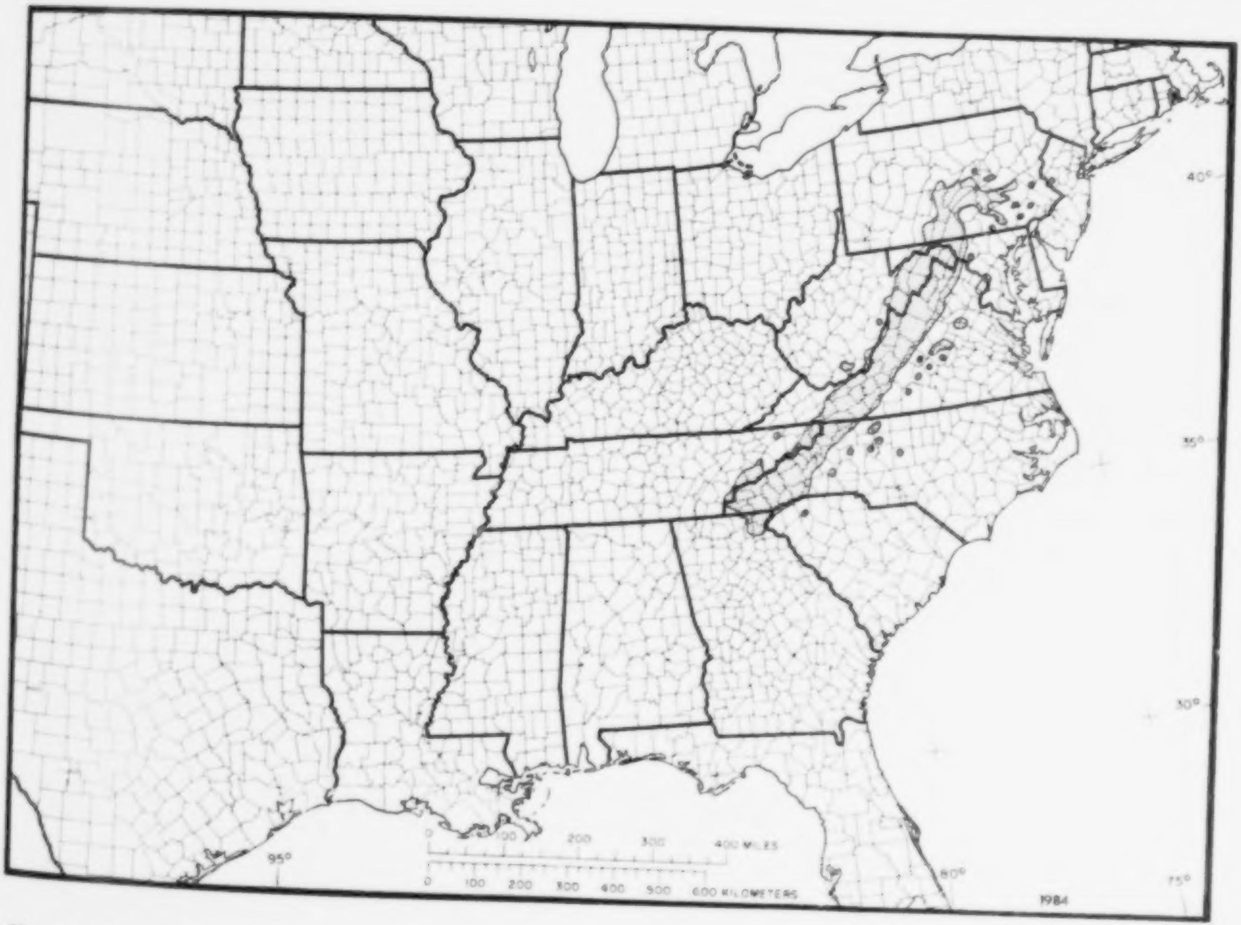

Figure 1—*The native range of Table Mountain pine.*

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rocky and shaly mountainous areas from Georgia into Pennsylvania *(8,16,17,29,31)*. It is frequently found on ridges of the precipitous gorges that dissect the Blue Ridge Mountains.

Table Mountain pine is unevenly distributed; its range extends from the Northern Appalachians in central Pennsylvania southwest to eastern West Virginia and southward into the Southern Appalachians, ending on the steep western edge of the mountains of North Carolina and east Tennessee *(1,2,6,9,10,11,19,25,29)*. To the east and south, its range includes the crest and eastern escarpment of the prominent Blue Ridge Front with its numerous rocky gorges and torrential mountain streams. Toward the southern end of its range, Table Mountain pine reaches its highest elevation of 1760 m (5,780 ft) in the Great Smoky Mountains *(8,16,29)*. There are numerous outlying populations of Table Mountain pine to the east and a few to the west of the Appalachians; many outliers are associated with monadnocks which rise considerably higher than the surrounding Piedmont *(5,6,23,24,30)*.

Climate

Precipitation within the range of Table Mountain pine varies with latitude and elevation. Warm season rainfall from April through September varies annually from 460 to 610 mm (18 to 24 in) in Pennsylvania to 690 to 990 mm (27 to 39 in) in the Southern Appalachians *(27)*. Mean annual precipitation ranges from 760 mm (30 in) in Pennsylvania to more than 2030 mm (80 in) in the Great Smoky Mountains. At the northern end of the range, average July temperature varies from 21° to 27° C (70° to 80° F); in the Great Smoky Mountains, the range is 15° to 21° C (60° to 70° F). Average January temperatures in Pennsylvania range from -7° to -1° C (20° to 30° F); in the Great Smoky Mountains, 2° to 5° C (35° to 40° F). In Pennsylvania, the average number of frost-free days varies from 150 to 170, and in the mountains of Tennessee, North Carolina, and north Georgia, from 170 to 180.

Soils and Topography

In Pennsylvania, Table Mountain pine grows on substrates of upper Silurian and lower Devonian rocks. Elsewhere it is known to grow on substrates of the Unicoi, Alligator Back, Loudon, Weverton, Erwin, Pottsville, Chemung, Pocono, Portage, and Hampshire or Catskill Formations *(17,31)*. Table Mountain pine is not found over limestone substrates. Although surface rock varies in Table Mountain pine stands in the Great Smoky Mountains, it is often less than 15 percent of total surface cover; however, on narrow ridges, surface rock can range from 35 to 55 percent or more *(16)*. In about half the stands bedrock occurs less than 50 cm (20 in) below the soil surface. Large amounts of gravel and rocks up to 30 cm (12 in) or more commonly occur in the solum; stone content has been found to range from 24 to 59 percent of air-dry weight *(31)*.

Some eleven soil series and rough stony land are associated with Table Mountain pine stands *(16,28,31)*. The most common soil series are Ashe, DeKalb, Ramsey, and Porters. In the Great Smoky Mountains, 57 percent of associated soils are Lithic Dystrochrepts, and 43 percent Typic Dystrochrepts of the order Inceptisols. Generally, A-horizon soils contain an average of 61, 28, and 11 percent sand, silt, and clay, respectively. Most of the B-horizon textures are loams and silt loams; silty clay loam occurs infrequently. Litter depth is about 5 cm (2 in). Organic matter content of the A horizon averages 5.5 percent, and in the B horizon 2.5 percent. Soil pH varies from 4.0 to 4.4 for the A and B horizons, respectively. Water-holding capacity in the solum ranges from 5 to 16 percent. Average nutrient content of a 15-cm (6-in) thick A horizon is as follows: calcium 120 kg/ha (107 lb/acre), magnesium 30 (27), phosphorus 5.8 (5.2), potassium 102 (91), and manganese 40 (36). In the B horizon, nutrient content averages are as follows: calcium 50 kg/ha (45 lb/acre), magnesium 27

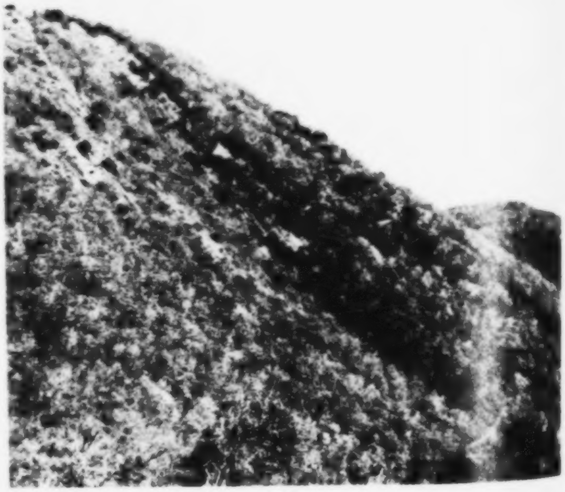

Figure 2—*A stand of Table Mountain pine (dark diagonal band near center of photo) in northwestern North Carolina at an elevation of 1035 m (3,400 ft), on a micaceous formation. Soils are shallow on this xeric southwest-facing site. The pines are extremely limby, about 20 cm (8 in) in d.b.h., and 8 m (25 ft) tall.*

(24), phosphorus 7.6 (6.8), potassium 76 (68), and manganese 24 (21). Nitrate and ammonium of the A horizon amount to 2.0 and 19 p/m, respectively; B-horizon values are slightly less. Generally, Table Mountain pine stands grow on soils that have minimum profile development and are shallow, stony, strongly acid, excessively drained, infertile, and of low productivity.

Table Mountain pine can grow over a wide range in elevation. Known extremes are 46 m (150 ft) in Delaware and 1762 m (5,780 ft) in the Great Smoky Mountains *(16,31)*; most often it occurs between 305 and 1220 m (1,000 to 4,000 ft) above sea level. In the Great Smoky Mountains, elevation affects the distribution of Table Mountain pine and Table Mountain pine-pitch pine stands *(8,16,29)*. Above 1060 m (3,480 ft) Table Mountain pine-pitch pine stands were mostly restricted to south-facing ridges; with increasing elevation, pitch pine decreased in abundance. Dominance of Table Mountain pine stands occurred at elevations above 1300 m (4,270 ft). On typical sites, the southwest-facing aspect is of critical importance to the presence of Table Mountain pine (fig. 2) although the species can and does grow on other aspects *(16,17,31)*. Slopes on which it occurs in the Great Smoky Mountains average 42 percent *(16)*.

Table Mountain pine has been found growing on an island in the Susquehanna River in southern Pennsylvania where the roots were continuously washed by water. It has also been seen around bogs on Mount Pisgah, NC, and at Big Meadows, Shenandoah National Park, VA *(31)*.

Associated Forest Cover

In Table Mountain pine stands of the Great Smoky Mountains associated tree species are red maple *(Acer rubrum)*, blackgum *(Nyssa sylvatica)*, sourwood *(Oxydendrum arboreum)*, pitch pine *(Pinus rigida)*, and chestnut oak *(Quercus prinus)*. In Table Mountain pine-pitch pine stands, additional associated species include scarlet oak *(Q. coccinea)*, American chestnut *(Castanea dentata)*, and black locust *(Robinia pseudoacacia) (16)*.

Table Mountain pine is also a minor associate in five forest cover types: Pitch Pine (Society of American Foresters Type 45), Shortleaf Pine (Type 75), Chestnut Oak (Type 44), White Pine–Chestnut Oak (Type 51), and Virginia Pine–Oak (Type 78) *(13)*. In the Shortleaf Pine type, Table Mountain pine is included only in the mountains; other associates are pitch pine, eastern hemlock *(Tsuga canadensis)*, black, white, southern red, scarlet, chestnut, post, and blackjack oaks *(Quercus velutina, Q. alba, Q. falcata, Q. coccinea, Q. prinus, Q. stellata,* and *Q. marilandica*, respectively), hickories *(Carya* spp.), and blackgum. In the Virginia Pine–Oak type, associated species in the foothills include shortleaf pine *(Pinus echinata)* and pitch pine, black, white, scarlet, chestnut, post, and blackjack oaks, hickories, and blackgum *(13,30,31)*.

The lower canopy vegetation in Table Mountain pine stands *(8,16,31)* includes rosebay rhododendron *(Rhododendron maximum)*, Catawba rhododendron *(R. catawbiense)*, Piedmont rhododendron *(R. minus)*, mountain-laurel *(Kalmia latifolia)*, mountain winterberry *(Ilex montana)*, hobblebush *(Viburnum alnifolium)*, blueberries *(Vaccinium* spp.), sawbrier *(Smilax glauca)*, greenbrier *(S. rotundifolia)*, fetterbush *(Pieris floribunda)*, white-alder *(Clethra acuminata)*, black huckleberry *(Gaylussacia baccata)*, bear huckleberry *(G. ursina)*, wild grape *(Vitis* spp.), and male blueberry *(Lyonia ligustrina)*. Mean shrub cover in the Great Smoky Mountains amounted to 65 percent in Table Mountain pine stands and 84 percent in Table Mountain pine-pitch pine stands.

Bear oak *(Quercus ilicifolia)*, mapleleaf viburnum *(Viburnum acerifolium)*, and low sweet blueberry *(Vaccinium angustifolium)* are most important stand components only in the northern part of the range of Table Mountain pine. Among tree species, black oak is important only in the north; blackjack oak and sourwood, in the south. Black birch *(Betula lenta)* is an associate only on rocky, nonshale areas, but Virginia pine is an associate at lower elevations, especially on shale. The evergreens, trailing arbutus *(Epigaea repens)* and galax *(Galax aphylla)*, are important only south of Virginia. Understory species in Table Mountain pine stands stabilize the shallow soil surrounding the pines.

Life History

Reproduction and Early Growth

Table Mountain pine needs stand and site disturbance, light, and heat for successful regeneration. In closed stands on western and northern exposures, Table Mountain pine cones are distinctly serotinous, but on southerly and easterly exposures many cones open soon after maturing. A large number of closed cones remain on the trees from 5 to 25 years and the retained seeds remain viable for 9 or more years *(21,32)*. After logging, residual trees are exposed to increased light and heat favorable for cone opening and seed dissemination. Often as much as 80 percent of the reproduction on logged-over areas is Table Mountain pine. In undisturbed stands, pine reproduction is periodic and often in scattered patches *(16,29,31)*. In Table Mountain pine-pitch pine stands under undisturbed conditions, especially without fire, successional trends toward increases in red maple, blackgum, and various oaks have been noted in the Great Smoky Mountains, with successional change strongest at lower elevations. In addition, the typical heavy heath layer in such stands results in low seedling densities and a lack of high frequencies for any species. Maintenance of natural Table Mountain pine stands can be most often ascribed to periodic fire. On very dry sites, the pines may represent an edaphic climax *(4,7,8,16,29,31)*. Other natural agents that lead to regeneration establishment are soil creep, cloudbursts, and forms of windthrow *(17)*.

Flowering and Fruiting—Table Mountain pine is monoecious. Cones are commonly seen on trees of sapling size and minimum seed-bearing age is 5 years. In northwestern North Carolina, pollen release at 457 m (1,500 ft) elevation begins the last week of March and ends during the first week of April; at 762 m (2,500 ft), pollen release begins about the second week in April and ceases near the end of the third week. Growth and reproductive activities of Table Mountain pine generally occur as early as, or earlier than, those of associated species *(31)*. Table Mountain pine is reproductively isolated from other pine associates by early pollen release, so hybridization is restricted.

The staminate cones of Table Mountain pine are a reddish purple *(31)*. The pollen is very large for eastern pines, being 50.2 ± 4.6 µ in inside diameter. The cone is heavy and egg shaped; the scales are much thicker at the ends and are armed with stout, hooked spines. Young ovulate strobili have a peduncle about 1 cm (0.4 in) long which is visible at maturity; as branch diameter increases, cones appear sessile *(32)*. From two to seven cones are often arranged in whorls on branches, around the stems of saplings, or on leaders *(21,25)*. Cones average 72 mm (2.8 in) in length, ranging from 42 to 103 mm (1.7 to 4.1 in); 54 mm (2.1 in) in width, ranging from 33 to 75 mm (1.3 to 3.0 in); and 64 cm^3 (3.9 in^3) in volume, ranging from 27 to 134 cm^3 (1.6 to 8.2 in^3). Cone dimensions and degree of serotiny decrease with increased elevation. Cones are largest at northern latitudes. In general, cones at higher elevations are well developed. Immature cones are deep green to brown, ripe cones are lustrous light brown, and old cones retained on branches are gray. Cones ripen in autumn of the second season; cone opening depends upon the degree of serotiny.

Seed Production and Dissemination—The seeds of Table Mountain pine are more or less triangular *(32)*. They average 5.3 mm (0.2 in) long, 3.1 mm (0.12 in) wide, and 13.8 mg (894 grains) in weight. Wing length varies from 19 to 25 mm (0.7 to 1.0 in) and wings are about 7 mm (0.3 in) wide; they range from a transparent light tan to dark brown. Seed coat roughness varies from smooth to a wartlike surface; the seed coat may be ridged. Cones averaging 58 mm (2.3 in) long and weighing 45 g (1.6 oz) produce about 50 seeds per cone, with an average viability of 81 percent. A bushel of cones contains about 0.18 kg (0.4 lb) of seeds. Cleaned seeds average 75,240/kg (34,200/lb) with a range of 67,540 to 83,600/kg (30,700 to 38,000/lb). A temperature range of 16° to 32° C (60° to 90° F) for 30 days is required to extract seed from cones *(26)*; kiln drying expedites the process. Seed weight without coat is about 7.6 mg (0.0003 oz); these large seeds may have adaptive value in drier regions, giving Table Mountain pine an advantage in establishing seedlings *(31)*. Frosts, drought, and heavy rains exert a greater influence on flower initiation, cone growth, seed development, and viability than tree age *(21)*. Although cones shed their seeds very irregularly, large numbers of seeds are disseminated annually.

Seedling Development—Table Mountain pine seed kept at 24° C (75° F) for 8 hours daylight and at 5° C (40° F) for 16 hours darkness in sand and peat has shown 65 percent germinative capacity with no pretreatment stratification *(26)*. Germination is epigeal. There can be four to nine cotyledons per seedling *(32)*. At 0.5 and 1.5 years, northern sources have a higher rate of water loss at high soil moisture contents than southern sources. Rate of water loss from seedlings with primary needles is greater than from seedlings with secondary needles *(31)*. Growth of seedlings can be increased by adding calcium and magnesium as soil amendments; other fertilizers have not been tried.

Of the three dry-site pines, Table Mountain pine roots are most affected by temperature; it grows a longer root than Virginia pine only between 16° to 28° C (61° to 82° F); pitch pine seedlings have the shortest roots at all temperatures *(31)*. Small top size to root length during seedling establishment would probably be the optimal condition for dry-site survival. Table Mountain pine grows more slowly without mycorrhizae, the root-shoot ratio of nonmycorrhizal seedlings is larger than that of mycorrhizal seedlings. Number of mycorrhizal types was higher in limed than unlimed soil, but liming caused no change in numbers of mycorrhizae *(31)*.

Competition from other vascular plants is probably an important factor in determining the distribution of the species, especially during establishment. Table Mountain pine occurs on areas least favorable for rapid plant growth; these harsher sites seemingly limit its early growth less than that of other species, thus allowing it to develop fast enough to compete successfully for canopy space, minerals, and soil moisture. The roots of very young seedlings are longer than that of pitch pine, and 0.5-year-old seedlings have lower transpiration rates *(31)*. Seedlings of Table Mountain pine develop mature needle fascicles earlier than Virginia pine seedlings.

Another advantage shown by this species is that seedling height growth and twig and needle elongation occur earlier than in pitch and Virginia pine during the period of least drought stress. The ultimate size of Table Mountain pine on xeric sites is constrained less than that of other tree species, allowing the pine to continue to compete, which it could not do on more fertile sites where hardwoods dominate. Growing conditions associated with poor oak growth characterize Table Mountain pine habitat.

Table Mountain pine is regarded as intolerant of shade, even more so than pitch and Virginia pine. The shrub stratum presents greatest competition for seedlings *(16)*, and generally, no seedlings of Table Mountain pine occur on sites without exposed mineral soil. Without fire and anthropic disturbances, Table Mountain pine would probably be found only on extremely dry and sterile rock outcrops and steep shale slopes, where the overstory canopy would be quite open and litter cover would never remain complete *(31)*.

Vegetative Reproduction—The prominent epicormic sprouts protruding from the bark of pitch pine are absent in Table Mountain pine; also absent are the dormant buds that occur along the bole and branches of pitch pine—an adaptation which allows recovery from defoliation. Table Mountain pine also has fewer basal buds than pitch pine; basal buds sprout after injury to the stem, allowing recovery of saplings after fire injury and animal damage *(31)*. Table Mountain pine seedlings of natural origin usually have a crook just above or just below ground level which may serve to protect the basal buds against fire.

Sapling and Pole Stages to Maturity

In an average stand of Table Mountain pine in the Great Smoky Mountains, the species dominates the overstory except that about 8 percent pitch pine is present *(16)*. Within such stands, the canopies are typically discontinuous and are composed of short, small-crowned trees of poor form. A maximum age of 250 years seems reasonable for Table Mountain pine (a counted age of 227 years has been recorded), a maximum diameter of 94.5 cm (37.2 in) and a maximum height of 29 m (95 ft) have been reported *(31)*. The general canopy height in the Great Smoky Mountains ranges from 8 to 12 m (26 to 39 ft), with a majority of canopy stems under 25 cm (9.8 in) d.b.h.; rarely are stems larger than 35 cm (13.8 in). Elsewhere, trees are generally less than 20 m (66 ft) tall and 40 cm (15.7 in) d.b.h. *(7,15)*. Live crowns often average more than 60 percent of total height, and limb-free bole length averages 12 percent *(31)*.

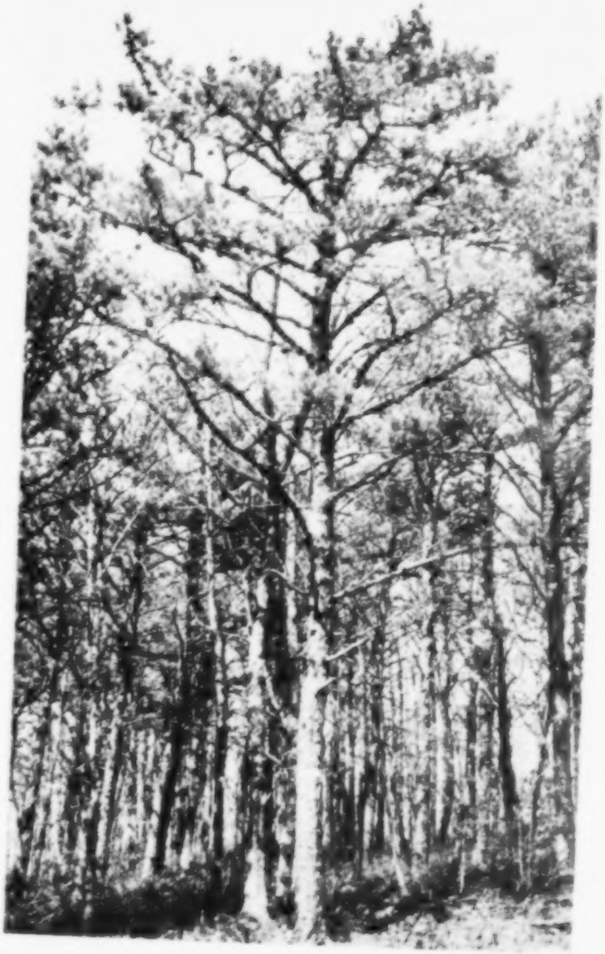

Figure 3—*Stand of Table Mountain pine.*

Table 1—Inventory of Table Mountain pine growing stock combined for Virginia, North Carolina, Tennessee, and Georgia *(20)*

D.b.h. class	Number of trees	Merchantable stem volume in thousands[1]		Sawlog volume in thousands[2]	
	thousand	*m^3*	*ft^3*	*m^3*	*fbm*
15 cm or 6 in	5,633	606	21,399	—	—
20 cm or 8 in	4,315	913	32,256	—	—
25 cm or 10 in	2,201	994	35,140	550	96,509
30 cm or 12 in	1,379	858	30,320	568	103,110
36 cm or 14 in	882	660	23,308	557	97,648
41 cm or 16 in	257	242	8,557	226	39,623
46 cm or 18 in	77	104	3,687	113	19,829
51 cm or 20 in (Virginia only)	23	36	1,268	45	7,870
53 to 71 cm or 21 to 28 in (North Carolina only)	22	29	1,016	36	6,400
Total	14,789	[3]4442	[3]156,951	2115	370,989

[1] Includes West Virginia.

[2] International 0.25-inch log rule.

[3] An additional 176.8 thousand m^3 (6,243 thousand ft^3) is found in Pennsylvania.

Much of the growth of Table Mountain pine goes into branch production (fig. 3).

Saplings are abundant, amounting to about 2,000 stems per hectare (809/acre) in the stands, and represent some 14 tree species. As in the canopy, Table Mountain pine saplings compose the majority of saplings. Saplings can vary in form from bushlike when open grown to slender, small-limbed trees in dense stands *(16,31)*.

The typical dense heath layer in Table Mountain pine stands severely restricts seedling densities and development and prevents high frequencies for any species. Stands are basically self-maintaining but severe fire is necessary to regenerate them where there is dense heath cover. Stands appearing to be permanent are associated with shallower litter, more rock outcrop, and have less basal area than stands more obviously successional.

Mature pitch pines are more resistant to fire damage than Table Mountain and Virginia pines because they have thicker bark. Table Mountain pines are intermediate in fire resistance and bark thickness. The thin-barked Virginia pines are least fire resistant *(16,31)*.

Growth and Yield—Stand and stocking values for Table Mountain pine are shown in table 1 by diameter classes. The table shows that trees in the largest d.b.h. classes are in Virginia and North Carolina; this peculiarity of distribution of large trees may be due to differences in the time of stand establishment caused by fire or insect kills.

In the southeastern mountains, Virginia has the largest area occupied by Table Mountain pine; the species accounts for 3.4 percent of all trees on the Jefferson National Forest in Virginia *(15)*. Georgia has the least acreage, but average volumes per unit area increase southward from Virginia, with 165.8 m^3/ha (2,368 ft^3/acre), to Georgia with 282.0 m^3/ha (4,028 ft^3/acre), probably because of more growing season precipitation, higher temperatures, and longer frost-free periods in stands growing farther south. Because of the large area and volume of Table Mountain pine in Virginia, this State grows and cuts more than other States; the species is virtually nonexistent as a viable timber type in South Carolina mountains and is at a very low volume in Georgia *(20)*.

Rooting Habit—Table Mountain pine seedlings are generally anchored into a rock crevice by their taproot *(7,15)*. Secondary or lateral roots then spread through the available soil and litter cover, taking up both moisture and nutrients. Other sinker roots descend into additional crevices, utilizing accumulated soil and the thin skins of finely weathered, nutrient-rich, moist soillike rock which coat the crevice surfaces: In this way the trees can survive on the most xeric sites.

Another adaptation to xeric sites shown by isolated or sparse trees is the production of extremely long branches—even longer than the height of the tree, where the lowermost ones sweep downward, often touching the ground *(31)*. These branches shield the underlying soil, rock, and roots from direct radiation and conserve soil moisture. Under such trees there is more protection against soil creep and the litter cover is relatively stable, with slow decomposition that contributes to available nutrient supplies and permits survival and growth under harshest conditions. Table Mountain and pitch pines are comparable in windfirmness; both surpass Virginia pine in this characteristic *(7)*.

Reaction to Competition—An overview of the natural range of Table Mountain pine indicates that it is not reproducing itself well and that regeneration is extremely scattered in patches in openings. Seedlings grow well, forming a dense sapling stand that attains its maximum growth rate at about age 30 when the trees are about 18 cm (7 in) d.b.h., but thereafter growth is exceedingly slow. Most of the present stands range from 60 to 100 years old; some originated after the severe beetle kills of the late 1800's and the fires that followed *(4,7,15,16)*.

The keys to successful natural regeneration of Table Mountain pine are heat and light *(21)*. It is classed as intolerant of shade. Even-age management precipitated by clearcutting, or in some cases, a seed-tree cut followed by a hot, fast-moving, prescribed fire to open cones without damaging enclosed seed, should suffice to regenerate it on harsh sites. A severe fire appears necessary for regeneration on sites with a heavy shrub layer *(31)*. It has least competition from associated species on shallow soils, erosion pavements, and rocky areas, and it is on such sites that its management can be most successful. On deeper soils, pitch and Virginia pine should be favored; where considerable microclimatic and soil variation occurs, a mixture of all three species would be best adapted to fully utilizing the site and offering protection against fire and other damaging agents. In remote areas where its perpetuation is desirable, small block or strip cuts on rocky southwesterly exposures with natural seedfall should suffice to regenerate it *(7,15,21,31)*.

Damaging Agents—Weather-related factors such as high gusty winds, glaze, heavy wet snowfall, cloudbursts, tornadoes, and lightning have been known to damage stands and isolated trees of Table Mountain pine *(7,15,17,31)*. The most serious diseases of Table Mountain pine are *Phaeolus schweinitzii*, which causes butt and root rot, and *Phellinus pini*, which causes heartrot in older or damaged trees *(18)*. *Dioryctria yatesi*, a cone-boring insect, can in some years destroy entire local seed crops. Periodically, the southern pine beetle, *Dendroctonus frontalis*, decimates entire stands *(3)*. The European pine sawfly, *Neodiprion sertifer*, at times defoliates trees of their previous year's needles, but seldom kills the trees. Trees of all sizes, from 3-year-old seedlings to mature specimens, are attacked by the pine twig gall scale, *Matsucoccus gallicola*, which causes bark to swell and crack, killing foliage and tree.

Special Uses

Table Mountain pine is used commercially for pulpwood, low-grade sawtimber, and firewood *(7,15)*. The serotinous cones on many trees make seed available for wildlife on a year-round basis. Many of the short stubby limbs seen on Table Mountain pine are caused by squirrels that prune off the cone-bearing section of the limb to get at seed in the heavily armed cone cluster *(22)*. Also, the heavy heath layer in Table Mountain pine stands provides plentiful wildlife food and cover *(16,31)*. The often gnarly Table Mountain pines are a welcome sight on rocky, clifflike areas of the Appalachians, but perhaps the most important use of the species is as protection forest; it stabilizes soil, minimizing erosion and runoff from the vast shale barrens and other rugged topographic features within its natural range *(17)*.

Genetics

Population Differences

The length–width ratio of Table Mountain pine needles is higher south of latitude 37° N. than north *(31)*. Stands in which most cones open the first and second year after ripening are in the northern end of its range. Seed weight is negatively correlated with elevation, but seedcoat characteristics and cotyledon number are not. There is no difference in specific gravity (0.470 unextracted cores) of Table Mountain pine over its natural geographic range *(12)*. In the Appalachian Mountains of southwest Virginia, in three stands of Table Mountain pine, as far as 42 km (26 mi) apart, there were significant differences in needle length, number of stomatal rows, and needle margin serrulations among trees and half-sib progeny within each stand *(14)*. In seedlings grown from seed from trees in the three stands, no significant differences among stands were observed for any of the characteristics measured.

Races and Hybrids

Racial variation, if any, among Table Mountain pines is not known.

Two hybrids of Table Mountain pine are known—*Pinus pungens* × *P. echinata* and *P. pungens* × *P. rigida*. In the former, the needles are long and there are two or three as in shortleaf pine, rather than the two, mostly intermediate in width, and twisted as in Table Mountain pine *(12)*. Needles of Table Mountain pine are stiff and prickly, while those of shortleaf pine are flexible; the intermediate needles of the hybrid are stiff and short pointed, but not prickly. The cones are small as in shortleaf pine, but intermediate, and more like Table Mountain pine in keel of apophysis and spine length. A *P. pungens* × *P. rigida* natural hybrid from Pisgah Ridge in Henderson County, NC, had external needle characteristics of Table Mountain pine, a cone intermediate in size and development of apophysis and umbo, and a dense group of short, small-diameter branches about 4.6 m (15 ft) up the bole, suggesting the sprouting characteristics of pitch pine *(31)*.

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Pinus radiata D. Don Monterey Pine

Pinaceae Pine family

Philip M. McDonald and Robert J. Laacke

Monterey pine (*Pinus radiata*) is the most widely planted pine in the world (*9*). Rapid growth and desirable lumber and pulp qualities cause it to be the leading introduced species in Australia, New Zealand, and Spain (*34*), and a major species in plantations of Argentina, Chile, Uruguay, Kenya, and the Republic of South Africa. In these countries, Monterey pine is a mainstay of the forest economy, serving internal markets, generating valuable foreign exchange reserves as an export, and reducing cutting pressure on native forests.

Pinus radiata was first noted by Thomas Coulter at Monterey, CA, in 1830. The scientific name refers to the strong markings on the cone scales, and the common name to the peninsula on which it grows extensively. Other common names are insignis pine and radiata pine. Radiata pine is a common name increasingly used worldwide; pino insigne is the Spanish equivalent.

Habitat

Native Range

Native stands of Monterey pine (fig.1) are found in three distinct areas of central-coastal California in San Mateo, Santa Cruz, Monterey, and San Luis Obispo Counties. The northernmost stand is east of point Año Nuevo, the central stand 48 km (30 mi) to the south near Monterey and Carmel, and the southernmost stand about 105 km (65 mi) away in the Pico Creek–Cambria area (*15*). Seldom is the pine found more than 11 km (7 mi) from the sea. The north–south range is about 209 km (130 mi). A close relative of Monterey pine also inhabits the northeastern portion of Guadalupe Island and the northern and central parts of Cedros Island—both of which are Mexican possessions. Guadalupe Island is 740 km (460 mi) south of Cambria, and Cedros Island is 908 km (564 mi) south–southeast of Cambria. Although trees on these islands differ in morphology from those in the United States, they have now been shown to be most closely related to *P. radiata* (*21*).

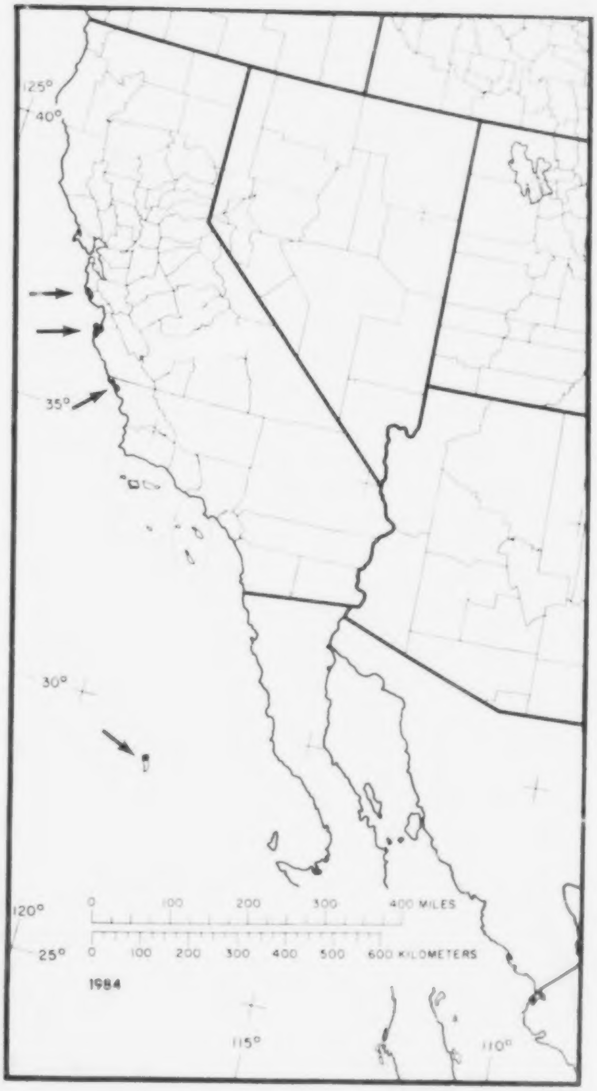

Figure 1—*The native range of Monterey pine.*

The area occupied by natural stands of Monterey pine on the United States mainland was once well defined, even though estimates of the total area ranged from 4860 to 6480 ha (12,000 to 16,000 acres) (*28*). Precise natural limits, however, are now difficult to determine because of conspicuous amounts of new regeneration. The southern part of the forest at Año Nuevo, for example, is estimated to have in-

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creased by as much as 95 ha (235 acres) in recent decades *(14)*. Additional trees have been planted, and these also have produced seed that led to many acres of new reproduction. Nevertheless, the total area currently occupied probably is no more than 8000 ha (19,770 acres) *(21)*.

Climate

The Monterey pine habitat is strongly influenced by its proximity to the Pacific Ocean from which the cold waters of southward-flowing currents result in high humidity, low temperatures, and summer fogs. The minimum relative humidity at Monterey in July, for example, averages between 60 and 70 percent *(23)*. At least one-third of the days each year are foggy *(35)*.

Temperatures tend to be mild, although extremes range from about -5° to 41° C (23° to 106° F). Mean monthly temperatures show a relatively even climate with a difference between the coldest and warmest month of about 6.5° C (12° F) in the range of 9° to 11° C (48° to 52° F) in winter and 16° to 18° C (61° to 64° F) in summer. Mean temperatures during the growing season, February through June, range from 11° to 16° C (52° to 61° F), with maximums of 17° to 24° C (63° to 75° F) *(34)*. Frost-free days number about 300 each year.

Annual precipitation ranges from about 380 to 890 mm (15 to 35 in) and varies from year to year. From December to March, precipitation averages 300 to 510 mm (12 to 20 in), with less than 50 mm (2 in) per month for the remaining months. Rain usually does not fall in July and August. During these months, however, the tree crowns collect moisture from fog that moves inland. Fog drip can amount to as much as 15 mm (0.59 in) per week at higher elevations on the Monterey Peninsula *(25)*. No snow falls in the natural range of Monterey pine. Año Nuevo is the wettest of the three mainland locales; Cambria, the driest; and Monterey, the foggiest *(3)*.

Wind is, at best, a minor climatic influence, averaging only 7.6 km/h (4.7 mi/h) on an annual basis. May is the windiest month, August the least windy *(23)*.

The climate of Guadalupe and Cedros Islands is Mediterranean-like, possibly with less rainfall and greater temperature extremes than for mainland stands. Fog is a critical factor and, on both islands, pine stands are restricted to foggy ridges and windward slopes, or occasionally to the moist slopes of deep canyons. On Cedros Island, fog was most frequent and of maximum concentration where the pines grew, and each pine grove tended to be covered with fog while the desert between was exposed to clear sky *(22)*.

Soils and Topography

In spite of a small and narrow natural range, Monterey pine grows on soils that are derived from a variety of parent materials. At Año Nuevo, for example, the underlying rocks are shales and marine sandstones. At Monterey, these rocks and granite are present, and at Cambria, parent materials are limestones, sandstones, cherts, and slates.

Monterey pine is found on soils of four orders. Mollisols are the most prominent and include four Haploxerolls (Santa Lucia, Ben Lomond, Catelli, and Baywood soil series) *(36)* and four Argialbolls (San Simeon, Conception, Watsonville, and Chamise series). Ultisols are next in extent and are represented by an Albaquult (Narlon series). The Entisol order is represented by one soil series, a Xeropsamment (Tangair series), and the Alfisol order by a Palexeralf (Tierra series).

At all three locations—Año Nuevo, Monterey, and Cambria—the soils have a number of similarities. Most soils are deep sandy loams, often derived from marine sediments. A thick accumulation of organic material is common beneath Monterey pine stands on good sites. The 8- to 15-cm (3- to 6-in) layer of organic material stores many times its weight in water and is a modest reservoir for nutrients. Most soils are found on sloping ground and are reasonably well drained, at least down to a clay layer at the 50- to 85-cm (20- to 33-in) depth. The clay layer is of critical importance. Pine roots generally do not extend far into this layer, but many penetrate for a short distance. Such roots have been observed to be well inoculated with mycorrhizae *(10)*. Another common attribute of soils supporting Monterey pine is that soil pH generally is acid, even extremely acid. Acidity often is high at or just above the clay layer. The combination of poor drainage and high acidity seems to enhance mycorrhizal formation. The clay layer, then, intercepts winter rains and forms a reservoir of water that is available for most of the year. Mycorrhizae on roots at or in the clay layer enhance the nutrient- and water-gathering capability of the pines. Of the seven most common mycorrhizal species that colonize the roots of Monterey pine seedlings in nurseries, *Rhizopogon rubescens* and *R. luteolus* enhanced height growth and nutrient uptake the most *(6)*.

In general, the topography on which Monterey pine grows is hilly and gently to moderately sloping. With one possible exception in the Santa Lucia Mountains, elevations range from sea level to about 305 m (1,000 ft). At the three mainland elevations, the most extensive stands are found on modest slopes or gently rolling terrain between the ocean and steeper inland hills. The pine is found on north aspects at all locations and shifts from all aspects at Año Nuevo, through presence only in sheltered canyons on south aspects at Monterey, to complete absence on all other aspects at Cambria. On Guadalupe and Cedros Islands, stands are found on gentle to steep slopes at elevational ranges of 300 to 1100 m (980 to 3,610 ft) on Guadalupe, and 275 to 640 m (900 to 2,100 ft) on Cedros *(21)*.

Limitations in habitat at each location probably contribute to the areal extent of the Monterey pine stands. At Año Nuevo, shallow soil near the coast could be limiting. At Monterey, lower rainfall together with differences in soil depth, texture, and location of clay layer could govern distribution. At Cambria, climate and soil mandate a shift from trees to grass and shrubs. Among the three mainland areas, where genetically controlled differences in tolerance to cold have been noted, the tolerance decreases from north to south *(16)*. Recently, analyses of satellite photos taken over several years have shown that the present groves of closed-cone pines "are all at centers of high fog concentrations" *(3)*. For the three mainland areas, the factor limiting the natural range of Monterey pine at its eastern boundary could be fog, but fog does not sufficiently explain the abrupt northern and southern termination of the pines' natural range. Farther south on Guadalupe and Cedros Islands, absence of fog appears to limit the distribution of the species. In spite of these evident limitations, the causes of restrictions on the range of Monterey pine are not clear.

Associated Forest Cover

Monterey pine has been listed in at least two vegetation classifications: the Closed-Cone Pine Forest Community of California *(27)* and the Closed-Cone Pine and Cypress Californian Floristic Province *(31)*.

The fossil record, although somewhat limited, indicates that this pine once occupied a larger range during the late Pleistocene epoch, extending almost continuously along the outer coastal strip and California islands. Fossil remains have been found at Tomales Bay, Little Sur, Carpinteria, Rancho La Brea, and Santa Cruz Island. The evidence suggests that present-day pines are survivors of an ancient oak-laurel, pine, and palm forest that grew well in a mild climate *(2)*.

Fire is a major influence affecting the extent and makeup of Monterey pine stands. Fire is frequent, sometimes of natural causes, often accidental, and sometimes deliberately set. Graziers at Cambria, for example, burned the woods to obtain more grass. At Año Nuevo, frequent fires have helped to maintain the pine forest. Without fire, the taller and longer-lived coast Douglas-fir *(Pseudotsuga menziesii* var. *menziesii)* would usurp land occupied by pines. Much regeneration and a number of even-aged stands at all three mainland locations can be traced directly to the influence of fire.

Many of the plant species associated with Monterey pine have been listed *(32)*. Such lists are subject to change because undisturbed stands are scarce; nearly all have been grazed, burned, or logged.

At Año Nuevo, tree associates of Monterey pine are coast Douglas-fir, redwood *(Sequoia sempervirens)*, knobcone pine *(Pinus attenuata)*, ponderosa pine *(P. ponderosa* var. *ponderosa)*, coast live oak *(Quercus agrifolia)*, and Pacific madrone *(Arbutus menziesii)*. Some portions of the Monterey pine forest are pure and almost fully stocked with 370 to 740 trees per hectare (150 to 300/acre). Width of tree crowns varies with age, but rarely are crowns interlocking. Monterey pine also intermingles with Douglas-fir on middle slopes and with knobcone pine and an oc-

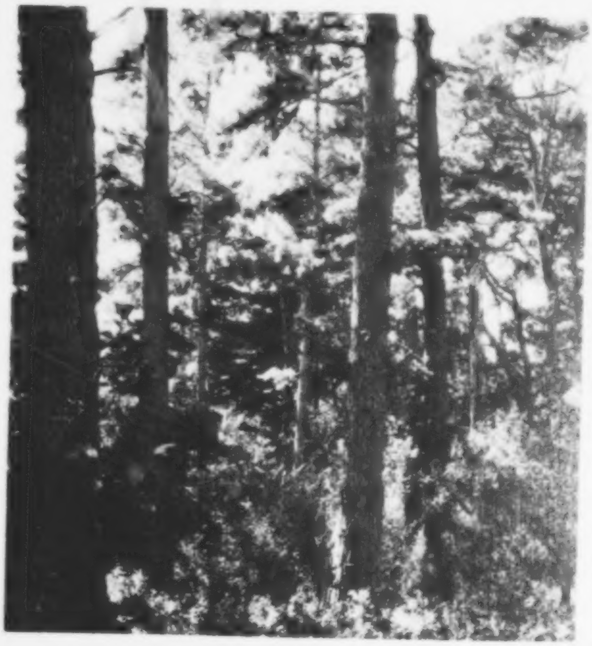

Figure 2—*An open mature stand of Monterey pine in the Año Nuevo Creek drainage with a poison-oak, California buckthorn, and California blackberry understory.*

casional ponderosa pine on upper drier slopes, especially where the soil is shallow and rocky. On lower slopes, redwood and an occasional madrone are present. Coast live oak, usually in the understory, also is an associate species. In some places, natural regeneration of Monterey pine is prominent, particularly where disturbance has bared the soil.

Understory associates generally are not particularly diverse nor abundant at Año Nuevo. In places, however, understory vegetation fully occupies the ground (fig. 2). In addition to young coast live oak, the most common species are bracken *(Pteridium aquilinum)*, poison-oak *(Toxicodendron diversilobum)*, coyotebrush *(Baccharis pilularis)*, blueblossom *(Ceanothus thyrsiflorus)*, California buckthorn *(Rhamnus californica)*, blackberry *(Rubus* spp.), coast sagebrush *(Artemisia californica)*, and several grasses.

At Monterey, tree associates are coast live oak, Monterey cypress *(Cupressus macrocarpa)*, Gowen cypress *(C. goveniana)*, and bishop pine *(Pinus muricata)*. Coast live oak is the most common tree associate of Monterey pine. Seldom taller than 9 m (30 ft), the oak usually is relegated to the understory. White alder *(Alnus rhombifolia)* and a species of willow *(Salix* sp.) are occasional associates in riparian zones. At least one species of willow is scattered throughout the forest on higher ground.

Shrubs and forbs in the Monterey forest vary with time after disturbance and general quality of the habitat. Successionally, young stands of pines, shrubs, and forbs often become established after fire. At age 45, Monterey pine has a stand density of 160 to 200 trees per hectare (65 to 81/acre). Shaggy-bark manzanita *(Arctostaphylos tomentosa)* and California huckleberry *(Vaccinium ovatum)* are prominent with an average cover of about 50 percent. By the time Monterey pine reaches age 65, competition, disease, and slow growth reduce its density to 80 to 120 trees per hectare (32 to 49/acre). In stands of this age, poison-oak, bush monkeyflower *(Mimulus aurantiacus)* and California blackberry *(Rubus ursinus)* are present and, along with the shrubs mentioned earlier, contribute to a shrub cover of about 40 percent. Openings form in the pine stand as the trees grow older but density remains about as before because younger age classes of pines contribute. Shrub cover continues at about 40 percent with poison-oak and creeping snowberry *(Symphoricarpos mollis)* becoming the understory dominants. In old stands where tree diameters are over 100 cm (39 in), one or more age classes of pine are present. Coast live oak sometimes constitutes 25 to 50 percent of the trees in such stands *(37)*.

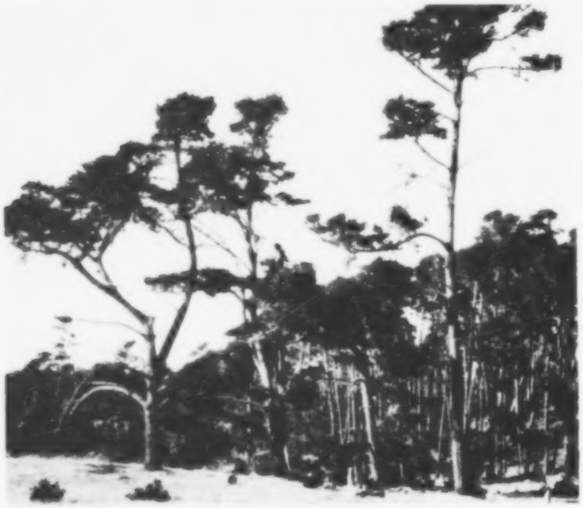

Figure 3—*Monterey pine on the grassy edge of its natural range near Cambria.*

At Cambria, tree associates of Monterey pine are limited to one hardwood: coast live oak. On better sites, understory vegetation near the typically open pine stands includes coast live oak, bracken, California blackberry, and poison-oak. On drier sites, coast sagebrush, coyotebrush, and bush monkeyflower are present. At the edge of the pine's natural range, grasses often are the only understory plants (fig. 3).

On Guadalupe and Cedros Islands, vegetation associated with Monterey pine is poorly known. That reported for Guadalupe Island is island live oak *(Quercus tomentella)*, Guadalupe Island palm *(Erythea edulis)*, and grasses; for Cedros, bishop pine, yucca *(Yucca* spp.), and at least two species of cactus *(Opuntia* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—In its native habitat, Monterey pine "flowers" in late winter and early spring. The species is monoecious; the numerous yellow male strobili are produced on side branches, and female flowers are produced in all parts of the crown. Monterey pine is multinodal and female strobili occasionally are found at a secondary whorl position *(18)*.

Seed Production and Dissemination—Fertile cones are produced as early as 5 to 10 years, but substantial crops are not yielded until age 15 or 20 if the trees are open-grown, and considerably later if the stands are dense. Cones mature in the autumn of the second season and most open during the first warm days of late winter and early spring. They range in color from lustrous nut brown to light brown when ripe, and in length from 8 to 18 cm (3 to 7 in). The ellipsoid seeds, jet black and pimpled, average about 2 cm (0.8 in) long. Monterey pines at Cambria have the largest cones and seeds; those at Monterey the smallest *(11)*. Each cone contains from 120 to 200 seeds.

Cones remain attached to the trees for many years and open and close several times, depending on temperature and humidity. Because the habitat of the species is typically cool and moist, cone opening is infrequent and of short duration, so that seeds are often retained and then disseminated over a longer period than in warmer and drier climates.

Although cones and seeds are produced almost every year, seedfall varies. A relatively small number of seeds dribble out of the cones each year. In warm and dry years, seedfall can be heavy. Fire is particularly effective for opening cones and releasing large quantities of stored seeds.

Several species of birds and small mammals depend in part for sustenance on the seeds of Monterey pine. Principal bird species are the scrub jay, Stellar jay, and common crow. Important small mammals are deer mice, chipmunks, and ground squirrels *(7)*. Numerous other creatures eat the seeds of this pine, but their effect usually is insignificant.

Seedling Development—Although the seeds of Monterey pine do not require stratification for good performance, germination is enhanced by it. Cold-moist stratification of 0 to 7 days is recommended for fresh seed and 7 to 20 days for stored seed. In one test with no pretreatment of seed, germinative energy was 16 percent in 7 days and germinative capacity 81 percent after 25 days at a controlled temperature of 20° C (68° F). In another test, again with no pretreatment, but where the day temperature was held at 30° C (86° F) and the night temperature at 20° C (68° F), germinative capacity was 67 percent after 28 days *(18)*.

Germination is epigeal. New germinants bear a whorl of five to nine cotyledons that are succeeded by primary needles. Secondary needles in fascicle bundles form when the seedling is a few months old. After age 3, the seedling produces only secondary needles. The root system of most seedlings consists of a slender taproot, aimed straight down.

Mycorrhizal associations with root tips in the upper 10 cm (4 in) of soil probably increase nutrient and water intake and enhance the growth of Monterey pine seedlings. At least 16 mycorrhizal fungi associated with Monterey pine have been identified in the United States and several others noted in other countries *(28)*.

The seedbed required for natural regeneration of Monterey pine is highly variable. The best seedbed is moist mineral soil free of competing vegetation. Numerous seedlings, however, are found where the seedbed consists of several inches of pine needles over mineral soil *(23)*. Although unknown, these seedlings could be the survivors of a great many seedlings and they could be much older than similar-sized, free-to-grow counterparts on bare mineral soil.

Seedlings develop best in full sunlight. Soil disturbed by logging and fire is conducive to seedling establishment and rapid growth. Dense slash decreases seedling density, although light slash can improve the seedling "catch."

Optimum conditions for regeneration, however, are produced by fire; maximum numbers of cones are opened, and at least a temporarily competition-free and receptive seedbed is prepared *(37)*. As a result, dense stands often are formed after burning. In fire-killed stands in foreign countries, Monterey pine seedlings were reported to number 1,235,500/ha (500,000/acre) and more than 2,471,000/ha (1,000,000/acre) *(32)*.

On Guadalupe Island, seedlings and saplings are scarce. "Very dense reproduction," however, was recorded in places on Cedros Island *(21)*.

Pines also become established in grassland vegetation and beneath live oaks, the latter providing shade during the critical establishment period. In most instances, the pines eventually grow through the oak canopy and dominate *(23)*. Some pines reproduce naturally under the canopies of older trees. Number and vigor of pine seedlings and saplings relate directly to the spacing of the older trees; the more dense the overstory, the fewer and slower growing the seedlings. Dense thickets often are formed in small openings.

Naturally established Monterey pine seedlings are fairly large initially and grow larger quickly. Seedlings 30 to 56 cm (12 to 22 in) tall after one growing season are common. Rapid shoot growth usually starts in February and continues until September. Monterey pine apparently begins growth at colder soil temperatures than associated conifers. Lack of soil moisture limits growth in the fall. The period of growth is variable, differing from tree to tree and from season to season *(23)*. By age 5, trees are about 6.6 cm (2.6 in) in d.b.h. and 6 m (20 ft) tall *(19)*. By this age, seedling roots have expanded much more laterally than vertically and have formed a lateral, rather than a taproot, system.

Artificial regeneration of Monterey pine in California is usually for horticultural rather than timber-growing purposes; however, several large plantations have been established for a variety of reasons. The most successful and long-lasting plantations are in central California near the Pacific Ocean *(28)*.

Monterey pine grows readily in California nurseries. Its only problem is rapid growth and stock too large for field planting. At one nursery, average seedling height was 41 cm (16 in), accumulating from the normal seeding date in April to lifting in January.

Seedling size and growth are affected by seed size, soil temperature, and soil moisture. After 32 weeks, Monterey pine seedlings were taller and heavier from seeds retained by a 0.39 cm (0.15 in) mesh screen than from seeds passing through a 0.33 cm (0.13 in) screen *(13)*.

Seedling root growth was greatest at 15° C (59° F), a value 5° C (9° F) lower than the optimum soil temperature reported for other pines. Monterey pines with a predawn water potential of –1.5 MPa (–15 bars) were unable to open stomates, a phenomenon also noted at a similar value for ponderosa and lodgepole *(Pinus contorta)* pines *(17)*.

Vegetative Reproduction—Monterey pine does not reproduce naturally from sprouts, and no record of sprouting in natural stands is known.

Reproduction from artificially rooted propagules of this pine has been successful in many trials in several countries. Hedging is one method for successfully mass-producing large numbers of symmetrical and straight cuttings and maintaining the juvenile nature of propagules *(22)*. Plantlets from embryos and cotyledons are another *(1)*.

Cuttings, or other means of vegetative propagation, offer a number of advantages over seedlings, not the least of which is closer control of genotype. Cuttings from mature planting stock show a reduced incidence of retarded leaders, excessive branching, crooked internodes, and frost susceptibility. Vegetative propagules also tend to have straighter boles, less forking, fewer and smaller branches, less bole taper, and thinner bark *(22)*. Height growth of cuttings generally is similar to that of seedlings, although extremes of environment and age of ortet can cause lower growth than from seedlings. Cuttings also develop a higher frequency of cones on the bole—a negative factor. This can be mitigated by pruning, however.

Sapling and Pole Stages to Maturity

Growth and Yield—On good sites, pine saplings that are free to grow and have at least moderate spacing enlarge rapidly: an increase in height of 1.2 to 2.4 m (4 to 8 ft) per year has been observed *(23)*. By age 15, trees are 24 cm (9.4 in) in d.b.h. and 16 m (53 ft) tall *(19)*. These values indicate a growth rate for the first 15 years that places Monterey pine among the most rapidly growing of American conifers. Although reproduction can be very dense, stands seldom, if ever, stagnate. A few saplings grow faster than their counterparts, quickly establish dominance, and eventually form the well-spaced, relatively open stands typical of older Monterey pine forests.

Branches of Monterey pine saplings die when shaded but persist on the bole for many years. In dense stands, the trunks clean themselves well *(35)*. Mature trees often have clear boles for 8 to 15 m (26 to 49 ft).

Height growth of pole-sized trees on poor sites may slow down appreciably after 15 years, but on better sites, it continues at a good rate until trees are about age 50 *(19)* At Monterey, pole-sized trees less than 30 cm (12 in) in d.b.h. average about 20 years old and 20 m (64 ft) tall. Height of mature trees ranges from 9 to 38 m (30 to 125 ft) but generally is 21 to 30 m (69 to 98 ft), with the tallest trees often found in small gullies. Diameters vary widely and, on a good site, average just under 64 cm (25 in) in d.b.h. A few trees reach an exceptional diameter of 122 cm (48 in) in d.b.h. At Cambria, Monterey pines are a little taller, averaging 30 to 37 m (98 to 121 ft) at maturity *(23)*.

On Guadalupe Island, the tallest tree was 33 m (108 ft); the largest d.b.h. recorded was 211 cm (83 in). On Cedros Island, the tallest tree measured 32 m (105 ft); the tree with the largest d.b.h. was 77 cm (30 in) *(21)*.

Crown development of Monterey pine is a function of age and spacing. In crowded conditions, the species has a narrow pointed crown. Vigorous trees continue to have pointed crowns until 35 to 45 years of age, after which the crown becomes flat and irregular. Trees 30 to 46 cm (12 to 18 in) in d.b.h. have crowns 5 to 6 m (16 to 20 ft) wide, but much narrower if crowded, and those larger than 76 cm (30 in) in d.b.h. have crowns 9 to 12 m (30 to 39 ft) wide. Trees taller than 30 m (98 ft) have a live crown one-third to one-sixth of this length *(23)*.

Monterey pine is short lived. It attains full size in 80 to 100 years and rarely lives beyond 150 years *(35)*.

Yield of Monterey pine in natural stands is lowered by the characteristically open spacing of the trees. Pine volume averages less than 281 m^3/ha (4,011 ft^3/acre). As stocking increases, so does productivity. A stand with better than average stocking, for example, averaged 490 m^3/ha (7,003 ft^3/acre). Trees were about 50 years old, 39 cm (15 in) in d.b.h. and numbered 408/ha (165/acre). The best stocked stand at Monterey contained 482 trees and 1681 m^3/ha (195 trees and 24,009 ft^3/acre). These trees averaged 52 cm (20 in) in d.b.h. and 29 m (95 ft) in height *(19)*.

In other countries, the yield of Monterey pine in plantations that are thinned and pruned and sometimes fertilized is much higher than that of natural stands. In New Zealand, stands 35 to 40 years old yield about 770 m^3/ha (11,004 ft^3/acre). On a productive site in Chile, trees 20 years old produce about 500 m^3/ha (7,145 ft^3/acre). They number about 270 trees per hectare (109/acre) after three thinnings, average about 48 cm (19 in) in d.b.h., and have been pruned three times *(30)*.

Rooting Habit—After age 5, the roots of pine seedlings grow downward as far as soil depth or the clay layer permit. Main support roots, however, develop in the top 61 cm (24 in), even in deeper soils *(23)*. Studies at Monterey and Cambria showed at least a few pine roots penetrated to 1.7 m (5.5 ft) in deeper soils *(8,10)*. The root system becomes extensive laterally and roots of mature pines extend from 9 to 12 m (30 to 39 ft) from the tree *(19)*. Where a layer of organic matter covers the soil, large numbers of small pine roots exploit the layer for moisture and nutrients.

The species is regarded as moderately windfirm on deeper soils but less so on shallow soils. Trees growing in soils saturated with moisture are vulnerable to windthrow, particularly in exposed places *(24)*.

Reaction to Competition—Because Monterey pine exists both as an overstory and an understory tree, it is classed as intermediate in tolerance to shade *(4)*—that is, at least as tolerant as any other pine in western North America. Age and site quality, however, affect this assessment. As a sapling or seedling, the species tolerates shade but becomes less tolerant in the pole stage and is intolerant when mature *(19)*. When overtopped, young pines can withstand a considerable amount of suppression, struggling along for 30 years or more before they die.

Damaging Agents—Within its restricted range, few abiotic factors cause significant damage except pollution, especially ozone. Because of its rapid growth, Monterey pine has been planted widely along the western coast of North America. In these plantings and even in the Central Valley of California, the pine technically is an introduced species because it is exposed to environmental conditions rare in its native range. Temperatures below freezing for only a few hours seriously damage and kill trees of all ages. Trees that are rapidly growing or newly planted are susceptible to windthrow during winter storms. Sudden increases in temperature to 38° C (100° F) or greater cause needle scorch and damage to new growth *(5)*.

Fire is a particular hazard to young, thin-barked trees and can be disastrous in dense plantations where persistent lower limbs become festooned with dead needles, resulting in an ideal situation for crowning fires. Pruning to a height of 2.1 to 2.4 m (7 to 8 ft) helps keep a fire on the ground and is a desirable measure for protection *(32)*.

Pathogens of significance in the natural range of Monterey pine include a dwarf mistletoe, two gall rusts, and two root diseases. Digger pine dwarf mistletoe *(Arceuthobium occidentale)* infects trees of all ages and is found in native stands except at Año Nuevo *(32)*. Western gall rust *(Peridermium harknessii)* and coastal gall rust *(P. cerebroides)* are found in the three stands in the United States and cause significant damage to young trees. Cedros and Guadalupe Island populations of Monterey pine have higher resistance to western gall rust than mainland populations *(29)*. A widespread pathogen of particular virulence is annosus root disease *(Heterobasidion annosum)*. Armillaria root disease *(Armillaria mellea)* is found where oaks are present, but damage to Monterey pine is minor.

Outside its natural range, Monterey pine is attacked by several pathogens in addition to those in native stands. Of these, the red band needle blight *(Scirrhia pini)* is the most damaging. This worldwide pathogen is not found in native stands but has caused serious damage and is a major concern for plantations in British Columbia, Washington, Oregon, and north-coastal California. Western gall rust is a pest in plantations from central California to British Columbia and can be damaging to Christmas tree plantations. As many as 35 other pathogens cause negligible to minor damage in exotic stands of Monterey pine *(5,32)*.

Furniss and Carolin *(12)* list 56 insects from 44 genera that feed on Monterey pine foliage, twigs, branches, and boles. Relatively few of these cause significant damage and only five can kill trees, especially those weakened by other agents. Four are bark beetles and one is a weevil; all are cambium feeders.

Bark beetle larvae mine the cambium of all but young trees. Once the trunk is girdled, the tree dies. All four species produce broods in stumps or fresh cut limbs and logs and commonly work in concert on individual trees. The Monterey pine ips *(Ips mexicanus)* is seldom a primary killer except in young plantations. The California four-spined ips *(I.*

plastographus) and pinyon ips *(I. confusus)* attack large and small trees. The red turpentine beetle *(Dendroctonus valens)* kills large, mature trees.

The Monterey pine weevil *(Pissodes radiatae)* is primarily a threat to young trees where the larvae mine cambium in tops, stems, bases, and even portions below ground.

Various other insects, including aphids, borers, caterpillars, and moths, cause minor damage. Probably the most serious of these is the Monterey pine cone beetle *(Conophthorus radiatae)* that attacks maturing cones in central California but does not damage the more southerly population.

Animal damage to ornamental plantings can be a problem but generally is not serious. On Guadalupe Island, however, chronic overgrazing by goats has virtually eliminated Monterey pine regeneration.

Special Uses

The wood of Monterey pine is light, soft, brittle, and coarse-grained. The trunk is characterized by a large amount of crook and other irregularities, a small percentage of clear bole, and frequent presence of disease. These characteristics cause the species to be of little commercial value for lumber and wood products in the United States. Past commodity use has been for coarse lumber in a localized market and for fuelwood. In marked contrast, the species is valued for wood products in many other countries.

A major use of this pine is as an ornamental in parks and urban areas. The species often is planted in areas devoid of trees where its rapid growth and attractive foliage quickly provide variety and contrast to the landscape. The pine also is planted extensively to help establish vegetative control of eroding and blowing soils. Prized as a living screen against wind, noise, and traffic, Monterey pine graces many a boulevard and backyard in urban areas. It also has been asexually propagated for Christmas trees *(33)*.

In its native habitat and particularly near the ocean, the rugged, picturesque, wind-battered trees deserve special mention for their esthetic appeal. Stands near Carmel, CA, are among the most photographed in the world.

Genetics

Population Differences

The three mainland populations of Monterey pine, although disjunct, grow where climate and soil are similar. A large proportion of the total phenotypic variation in several branch, needle, and cone characteristics, however, is observed between individual trees at each location. The Cambria population, although less variable than the other two, differs from them in several cone, branch, and needle characteristics. In Australia these differences, plus a slower growth rate and a different pattern of seasonal growth, suggest that the Cambria population differs genetically from the northern populations *(11)*. A recent study, however, indicates little genetic differentiation among the native populations. Most of the genetic variation is located within each stand *(26)*.

Hybrids

No evidence of widespread introgression from knobcone or bishop pine has been found, although hybridization is occurring locally between Monterey and knobcone pines at Año Nuevo *(11)*. The hybrid is designated *Pinus attenuata* × *radiata* Stockwell & Righter. The two-needled pine found on Guadalupe and Cedros Islands is currently named *P. radiata* var. *binata*.

The unique characteristics of rapid growth, large genetic variability, and ease of vegetative propagation have made Monterey pine the subject of intensive genetic improvement programs in several countries, notably Australia and New Zealand.

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Pinus resinosa Ait. Red Pine

Pinaceae Pine family

Paul O. Rudolf

Red pine *(Pinus resinosa)*, also called Norway pine, is one of the most extensively planted species in the northern United States and Canada. It is a medium-size tree with lightweight, close-grained, pale reddish wood used primarily for timber and pulpwood. Trees 97 cm (38 in) in d.b.h. and 43 m (141 ft) tall in Michigan are among the largest living specimens.

Habitat

Native Range

Red pine (fig. 1) is confined to the Northern Forest region and the southern fringe of the Boreal Forest region. It grows in a narrow zone about 2400 km (1,500 mi) long and 800 km (500 mi) wide around the Great Lakes and the St. Lawrence River, most of it within or closely adjacent to the area glaciated during the late Pleistocene *(76)*. Its range extends from Cape Breton Island, Nova Scotia, Prince Edward Island, New Brunswick, southern Quebec, and Maine, westward to central Ontario and southeastern Manitoba, southward to southeastern Minnesota and eastward to Wisconsin, Michigan, southern Ontario, northern Pennsylvania, northern New Jersey, Connecticut, and Massachusetts. It also grows locally in northern Illinois, eastern West Virginia, and Newfoundland *(53)*.

Climate

Red pine is native to areas with cool-to-warm summers, cold winters, and low to moderate precipitation. Within red pine's natural range the average January temperatures vary from -18° to -4° C (0° to 25° F) and the average July temperatures from 16° to 21° C (60° to 70° F). Average annual maximum temperatures range from 32° to 38°C (90° to 100° F), and average annual minimum temperatures range from -23° to -40° C (-10° to -40° F).

Average annual precipitation is from 510 to 1010 mm (20 to 40 in) throughout much of the range but reaches 1520 mm (60 in) in some eastern localities. The average growing season precipitation ranges from 380 to 640 mm (15 to 25 in), and the average annual snowfall ranges from 100 to 300 cm (40 to 120 in). Summer droughts of 30 or more days occur commonly in the western half of the range. The frost-free period ranges from 80 to 160 days, although it may be as short as 40 days northeast of Lake Superior in Ontario. The northern limit of red pine is related to length of frost-free period and closely parallels the 2° C (35° F) mean annual isotherm.

Soils and Topography

Natural stands of red pine are confined largely to sandy soils. They are most common on Entisols followed in order by Spodosols, Alfisols, and Inceptisols. Common materials are glaciofluvial and aeolian in origin, and lacustrine deposits and loamy and finer till soils are less frequently occupied. Red pine commonly grows on dry soils low in fertility, but it is also found on a variety of sites including organic debris over rock outcrops and some structured lacustrine red clays, where it may be somewhat stunted, however. Red pine is rarely found in swamps but is common along swamp borders. It does not grow where the surface soil is alkaline, although it grows on dry, acid soils overlying well drained limestones or calcareous soils. Although it can grow well on silt loams, red pine grows only sporadically on heavier soils, probably because of its inability to compete with more aggressive species and because of root injuries known to occur on some such soils. It grows especially well (height growth may be doubled) on naturally subirrigated soils with well aerated surface layers and a water table at a depth of 1 to 3 m (4 to 9 ft) in Wisconsin. Best plantation development is made on soils that range from moderately drained to those without substantial moisture stress *(8,11,16,24,55, 90,91,95,100)*.

In typical old growth stands in the Lake States the organic layer (L, F, and H layers) seldom builds up to a depth of more than 5 to 13 cm (2 to 5 in), and its ovendry weight increases with stand density from 12 300 to 84 100 kg/ha (11,000 to 75,000 lb/acre). Beneath is a gray, leached layer of sandy soil 15 to 20 cm (6 to 8 in) thick overlying a brownish layer of sandy soil 1 or more meters (3 or more feet) thick. Sometimes discontinuous bands or lenses of finer textured material are found at depths up to 3 m (9 ft) and their silt-plus-clay content improves the productivity of red pine. In dry summers almost all available moisture may be withdrawn to a depth of 0.6 to 2.1 m (2 to 7 ft) or more.

Red pine grows satisfactorily on soils that, in the upper 25 cm (10 in), have a pH of 4.5 to 6.0, a bulk

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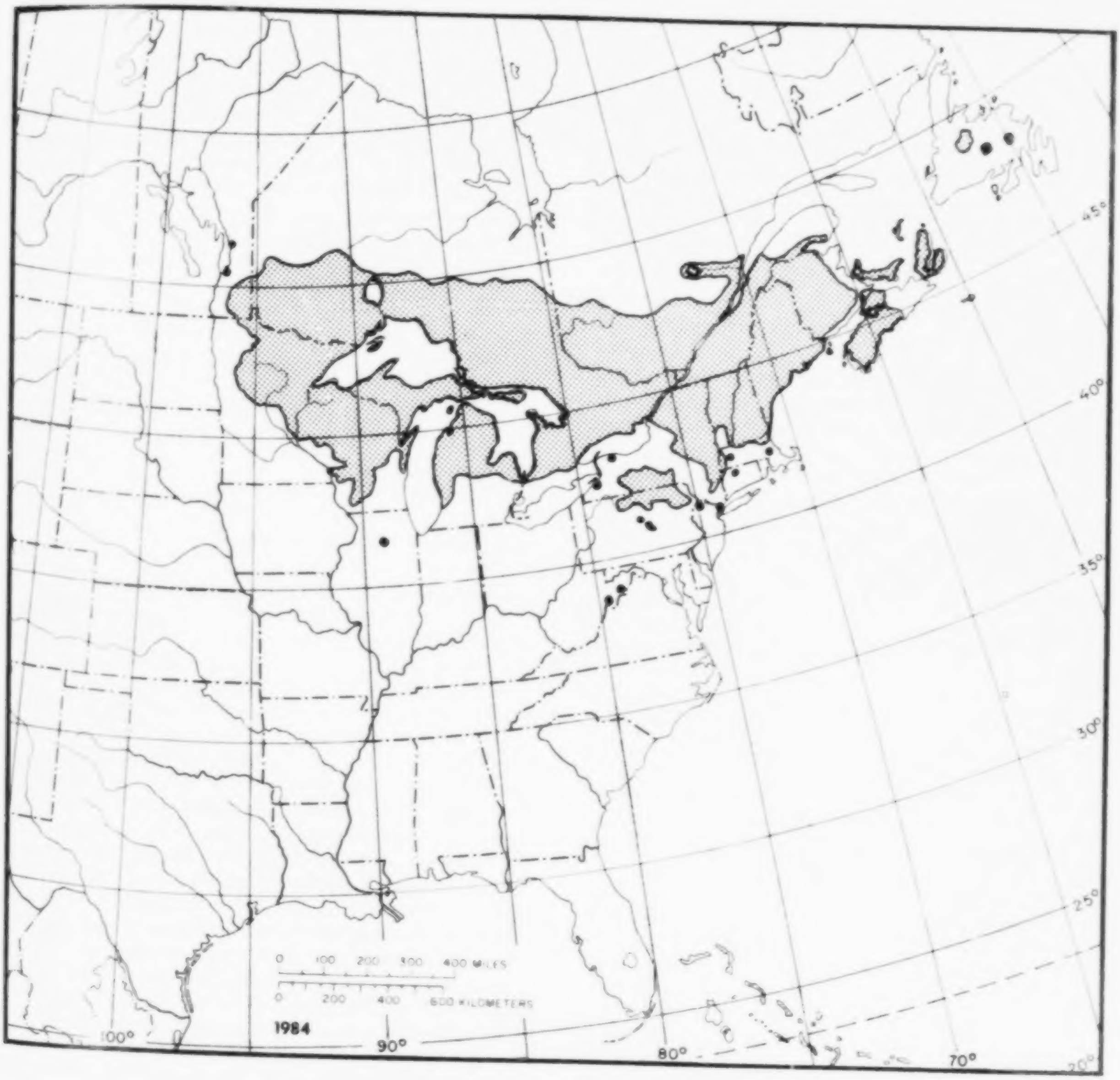

Figure 1—*The native range of red pine.*

density of about 1.30 g/cm^3 (0.75 oz/in^3), a silt-plus-clay content of 10 to 40 percent, available water storage capacity of 6 to 23 percent, a base exchange capacity of 2 to 11 milliequivalents (meq) per 100 g, organic matter content of at least 1.7 percent, total nitrogen content of 1100 to 1700 kg/ha (1,000 to 1,500 lb/acre), available phosphorus of 34 to 146 kg/ha (30 to 130 lb/acre), available potassium of 126 to 157 kg/ha (112 to 140 lb/acre), exchangeable calcium of 0.80 to 2.00 meq per 100 g, and exchangeable magnesium of 0.20 to 0.45 meq per 100 g *(3,4,5,12,36, 76,99)*.

In the Lake States and Ontario, red pine grows most commonly on level or gently rolling sand plains or on low ridges adjacent to lakes and swamps, at elevations from 240 to 430 m (800 to 1,400 ft) above sea level. In the East it is found not only on outwash plains but also on mountain slopes and hilltops. It grows chiefly at elevations between 210 and 400 m (700 to 1,300 ft) above sea level in New England, and up to 820 m (2,700 ft) in the Adirondacks.

The West Virginia outliers are found at an elevation of 945 to 1290 m (3,100 to 4,200 ft) above sea level. In Canada the production of red pine increases from pine ridges to pine plains to pine uplands *(44,76,87)*.

Associated Forest Cover

In parts of the northern Lake States, Ontario, and Quebec, red pine grows in extensive pure stands and in the Northeast and eastern Canada in small pure stands. More often it is found with jack pine *(Pinus banksiana)*, eastern white pine *(P. strobus)*, or both. It is a common component in three forest cover types: Red Pine (Society of American Foresters Type 15), Jack Pine (Type 1), and Eastern White Pine (Type 21) and is an occasional associate in one, Northern Pin Oak (Type 14) *(26,90)*.

On the coarser, drier soils, common associates of red pine are jack pine, quaking aspen *(Populus tremuloides)*, bigtooth aspen *(P. grandidentata)*, scrubby oaks (chiefly northern pin oak *(Quercus ellipsoidalis)*), and bear oak *(Q. ilicifolia)*. On somewhat better soils (fine sands to loamy sands), in addition to the foregoing, associates may be eastern white pine, red maple *(Acer rubrum)*, black cherry *(Prunus serotina)*, northern red oak *(Quercus rubra)*, white oak *(Q. alba)*, chestnut oak *(Q. prinus)*, balsam fir *(Abies balsamea)*, black spruce *(Picea mariana)*, and occasional specimens of the better hardwoods. On sandy loam and loam soils, red pine's associates include sugar maple *(Acer saccharum)*, eastern white pine, American basswood *(Tilia americana)*, red maple, balsam fir, paper birch *(Betula papyrifera)*, yellow birch *(B. alleghaniensis)*, American beech *(Fagus grandifolia)*, northern red oak, eastern hemlock *(Tsuga canadensis)*, white spruce *(Picea glauca)*, white ash *(Fraxinus americana)*, red spruce *(Picea rubens)*, northern white-cedar *(Thuja occidentalis)*, and eastern hophornbeam *(Ostrya virginiana)*. Growing with red pine in the West Virginia outlier are eastern white pine, pitch pine *(Pinus rigida)*, Virginia pine *(P. virginiana)*, table mountain pine *(P. pungens)*, sweet birch *(Betula lenta)*, northern red oak and bear oak. In northeastern Illinois the woody plant associates include northern red oak, white oak, American hornbeam *(Carpinus caroliniana)*, hackberry *(Celtis occidentalis)*, and roundleaf serviceberry *(Amelanchier sanguinea)*. All the associates of red pine grow only as understory except eastern white pine and occasionally jack pine or aspen. When found with hardwoods, red pine usually is a minor but dominant component of the stand *(76,87)*.

The most common shrubs associated with red pine include Canada blueberry *(Vaccinium canadense)*, low sweet blueberry *(V. angustifolium)*, sweetfern *(Comptonia peregrina)*, common bearberry *(Arctostaphylos uva-ursi)*, prairie willow *(Salix humilis)*, American hazel *(Corylus americana)*, beaked hazel *(C. cornuta)*, striped maple *(Acer pensylvanicum)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, New Jersey tea *(Ceanothus americanus)*, sand cherry *(Prunus pumila* and *P. susquehanae)*, fly honeysuckle *(Lonicera canadensis)*, serviceberries *(Amelanchier* spp.), raspberries *(Rubus* spp.), trailing arbutus *(Epigaea repens)*, and spireas *(Spiraea* spp.) *(26,76,87)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Red pine is monoecious; the flowers appear between April and June. The female flowers, 2 to 4 mm (0.1 to 0.2 in) long, are borne mostly in the middle third of the crown (in the upper third in older trees), and the purple male flowers, 10 to 20 mm (0.4 to 0.8 in) long, are borne in the lower crown. In Ontario and northern Minnesota, the cone first becomes visible in late May or early June, although the cone primordia are differentiated in June to August of the previous year. Pollination occurs during late May or early June when the cone is about 4 mm (0.2 in) long. By late summer the cone is 10 to 15 mm (0.4 to 0.6 in) long and stops growing for the season. Insects, weather extremes, and other damaging agents may cause the loss of 60 percent of the cones between the first and second year of their development. The remaining cones begin further growth the next spring, but actual fertilization does not take place until mid-July of the second year (13 months after pollination) when cone growth is completed and the fully developed seed coats have hardened. At that time the cone is 37 to 50 mm (1.5 to 2.0 in) long *(37,52,56)*.

Seedfall begins at the time cones ripen and continues throughout the winter and into the next summer, although the bulk of it can be deferred by cool, wet weather (which retards cone opening). The heaviest and most viable seed falls the first month. From year to year, soundness of the dispersed seed varied from 14 to 86 percent in Michigan and Manitoba; it was highest in the best crop years *(19,74,76,81)*.

Above-normal temperatures in April, July, August, and September, 2 years before cone maturity, favor cone production. Cone production is better on branches that are young, thick, long, and on the south side of the tree.

Many of the seeds are viable when the cones have become purple with reddish brown scale tips or have a specific gravity of about 0.80 to 0.94 (they float in kerosene), but they are not dispersed until the cones are completely brown (specific gravity about 0.60). The cones themselves usually fall the next spring or summer, although some may remain on the tree 2 or 3 years *(37,52,57,76)*.

Seed Production and Dissemination—Under favorable growing conditions planted red pines have produced staminate (male) flowers at age 9, ovulate (female) flowers at age 5, and viable seed at age 12. Normally, however, seed production begins at about 15 to 25 years in open grown trees and at 50 to 60 years for those in closed stands. Seed production usually is best in trees from 50 to 150 years of age with an average cone production per tree of about 18 liters (0.5 bushel). The final cone yield (number of survivors/number of female flowers initiated) ranges from 0 to 81 percent from year to year and often is only about 20 percent.

Good seed crops are produced at intervals of 3 to 7 years with light crops in most intervening years (about one year in four may have little or no seed production). Bumper cone crops are produced only once every 10 to 12 years *(31,56,76,90)*.

Only about 45 percent of the scales on a typical red pine cone produce viable seed. At the time of pollination a typical red pine cone has from 30 to 110 (average 60 to 90) ovules that are capable of becoming seeds, but only about half of them actually develop. Cones produced in the upper third of the crown produce more good seeds than those at lower levels, and cones borne on main branch terminals produce more than those borne on lateral terminals.

Cone production per tree improves as stand density decreases. The number of cones produced per tree in a mature medium-stocked stand during a good seed year averages 50 for unthrifty trees, 200 for medium trees, 400 for vigorous and partly open grown trees, and 725 for open grown trees. In seed production areas in the northern Lake States—with 200 to 250 trees per hectare (80 to 100/acre), there may be about 87,500 cones per hectare (35,000/acre) in a good crop year and 17,500/ha (7,100/acre) in a low crop year *(57,58,76)*.

In dense stands less than 20 percent of the trees may produce cones, and the seedfall may average less than 10 seeds per tree. Hence, thinning helps increase red pine cone production per tree, and the recommended average spacing between trees for seed production areas is one-half the average height of dominant and codominant trees. Applying fertilizers also may improve cone production on trees 45 years of age or older with well-developed crowns. Some trees are consistently good and others consistently poor cone producers. Up to 751,000 sound seeds per hectare (300,000/acre) have been found in southeastern Manitoba, and 2,767,000/ha (1,120,000/acre) in Minnesota *(19,20,23,30,74,76)*.

Seeds are light. Cleaned seed averages about 115,000/kg (52,000/lb) and ranges from 66,000 to 156,000/kg (30,000 to 71,000/lb).

The cones open best on hot, still autumn days when there is little wind to carry the seeds far. Seeds may be disseminated up to 275 m (900 ft) from the parent tree, but the effective range, as measured by established seedlings, averages about 12 m (40 ft).

Several factors may reduce red pine seed crops: prolonged rainy weather at the time of pollination; fire injury; many species of insects which consume the flowers and seeds or damage the cones; squirrels, mice, and other animals and several songbirds which eat the seeds or damage cone bearing branches; and an unidentified witches' broom *(49,76)*.

Seedling Establishment and Development—In nature red pine stands become established following fire, the only natural agent capable of providing most of the conditions required for natural red pine reproduction. Summer surface fires with an energy output rate less than 700 kW/m of front (200 Btu/(s·ft)) can provide a satisfactory seedbed, kill back some competing tree species, reduce brush competition the first few years, reduce cone insect populations, and produce an open overstory canopy. Given such a fire, other conditions such as the following would be required to ensure the establishment of a new red pine stand: a good red pine seed crop, not too thick a layer of ashes, weather conditions favorable for seed germination and seedling establishment, and subsequent freedom from fire for several decades. Based on observations of old growth stands in north-central Minnesota such a combination of conditions in a given locality may occur only about once in 75 to 100 years *(21,61, 76,96)*.

Germination is epigeal *(45)*. Most seedlings emerge when the temperature is from 21° to 30° C (70° to 86° F). In northern Minnesota, seedlings were established only in those years with rainfall more than 100 mm (4 in) for May, June, and July, or a little less if followed by good rainfall the latter part of the growing season. If rainfall is deficient, the seeds can lie over for 1 to 3 years before germinating. Occasionally a few seeds germinate in the fall. Heavy seeds produce heavier seedlings than do lighter seeds, and the heavier seedlings outgrow the lighter seedlings for at least the first 10 years.

Red pine seeds may germinate, but seedlings do not grow beneath dense brush, on heavy litter or sod, or on recent burns with a heavy cover of ashes. Germination is best under conditions that favor high moisture content in the seed, such as a fine sand seedbed, thin moss or litter, a water table within 1.2 m (4 ft) of the soil surface, some shade, abundant precipitation, and light covering of the seed. Germination is satisfactory at a range of soil reactions but is reduced at pH 8.5 or higher. Young seedlings grow best on soil media with good moisture retention, a high cation exchange capacity, and low pH—5.1 to 5.5. Germination is inhibited by full sunlight for 4 hours or more per day *(2,21,29,45,69,70,76)*.

Approximately 35 percent of full sunlight offers satisfactory conditions for red pine seedlings to become established and they can achieve maximum height growth in as little as 45 percent of full sunlight up to age 5. Establishment is uncertain with light values below 17 percent, although very young seedlings can exist in less than 3 percent light. Because decreasing light levels diminish root weight more than top weight, shade grown seedlings are smaller in all dimensions (stem length and dry weight of stem, foliage, and roots) except needle length than those grown in full sunlight, and the average rate of photosynthesis is higher in shade grown shoots. After they have grown above the sparse ground cover that favored germination and early survival, the number of seedlings per hectare seems to increase with light up to full daylight. The height growth of the red pine seedlings also increases with increasing sunlight up to 63 percent of full daylight, or up to 6 hours of full sunlight, and their dry weight increases up to full light *(44,54,76)*.

The age of the mother tree appears to affect the time of flushing in first-year seedlings; it is earliest in progeny of mother trees 80 to 120 years old, and later in progeny of trees less than 30 years old and trees more than 121 years old *(76)*.

The time that shoot growth begins and ends varies with the season within a locality and with the climatic conditions over the range of red pine. Reserves in old needles contribute up to 80 percent or more to total shoot elongation, and phloem-translocated reserves from main branches, main stem, and roots contribute most of the balance. Terminal shoot growth begins in the spring when the mean weekly air temperature is about 10° C (50° F) and the current soil temperature is from 13.3° C (56° F) at the surface to 5.6° C (42° F) at a depth of 61 cm (24 in); this growth is completed in 43 to 123 days depending upon the locality and season *(48,71,76)*.

The period of cambial growth begins a little later than shoot elongation and is only about two-thirds completed when shoot growth ceases. In seedlings, summer wood formation begins when needle elongation stops. The roots continue to grow after cambial growth stops. After this the needles reach their maximum growth rate, followed by a second high of cambial growth. After nearly all growth is completed and a full complement of needles is functioning, the roots reach a second maximum of elongation. Radial growth seems to be closely related to the precipitation of the current season, especially in the early part of the growing season *(25,76)*.

Red pine seedlings usually grow slowly in the wild, especially if they are shaded. At the end of the first year, wild seedlings often are less than 3 cm (1 in) tall. After 4 or 5 years the growth rate begins to increase, but seedlings usually take 4 to 10 years to reach breast height (1.37 m or 4.5 ft) and overtopped seedlings may take 15 to 16 years. For many years thereafter height growth may average about 0.3 m (1 ft) per year in the Lake States and Ontario and 0.5 m (1.5 ft) per year in the Northeast *(76,90)*.

The productivity of the site is reflected by the average annual height growth above breast height or better, above 2.4 m (8 ft), ranging from 25 to 66 cm (10 to 26 in) for poor to good sites *(6,13,76,90)*.

Vegetative Reproduction—In nature red pine does not reproduce vegetatively. Only with great difficulty can stem cuttings or leaf bundles be rooted artificially regardless of treatment, and no successful propagation of red pine by tissue culture methods has yet been reported.

As many as 84 percent of cuttings, taken during the summer from side branches of 3-year-old red pine seedlings, took root in sand under mist if the stock plants had been fertilized heavily and the cuttings had been treated with indolebutyric acid and water. The rooted cuttings at 1 year were equal to or better than 2-0 nursery grown seedlings *(76)*.

Dormant red pine scions kept overwinter at −18° C (0° F) can be field grafted successfully onto red pine and Scotch pine *(P. sylvestris)* stocks in the spring. Successful grafts also have been made on eastern white pine and Mugho pine *(P. mugo)*. Side veneer grafting of dormant scions on potted rootstock forced in the greenhouse in February has been successful in northern Wisconsin. Grafting is rarely successful on jack pine stocks. Semisucculent shoots from 12-year-old red pine trees were successfully cleft grafted on 9-year-old Scotch pine in the field: the shoots were collected and on the same day were

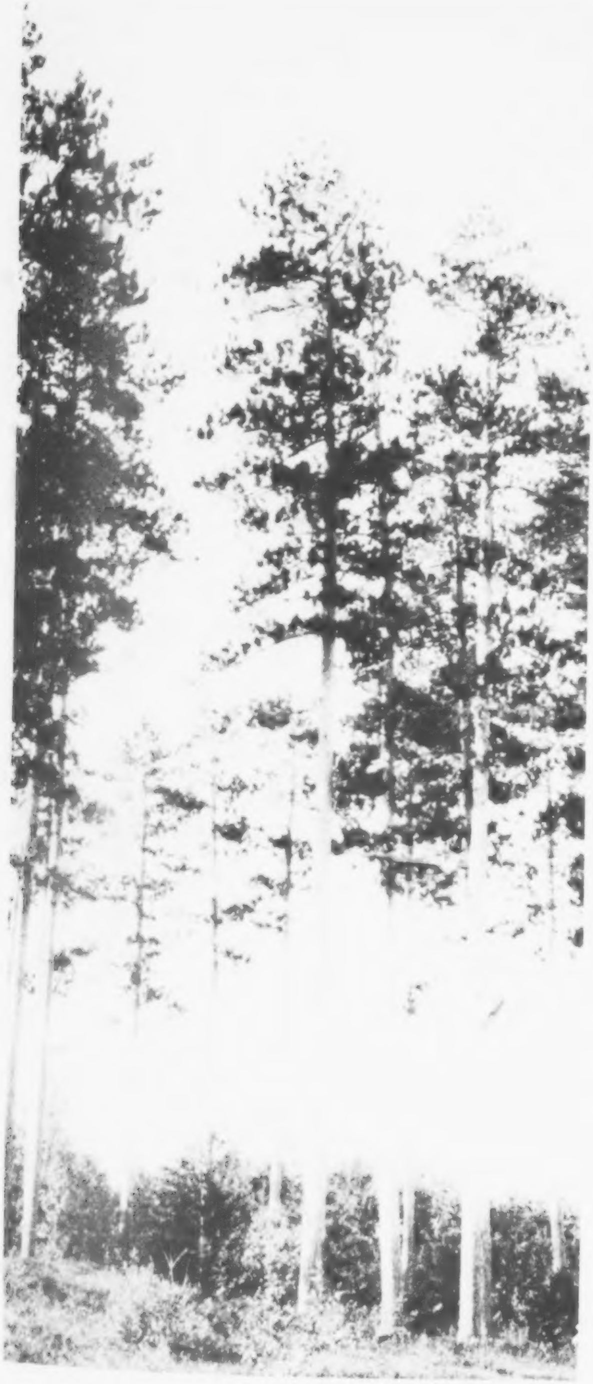

Figure 2—*Edge of stand in northern Lower Michigan, showing typical stem form and crown habit of mature red pine.*

grafted on current season's shoots that had just completed height growth. Incompatibility of interspecific grafts, however, appears to be a serious problem *(28,47,64,76)*.

Sapling and Pole Stages to Maturity

In the forest, red pine normally is a tall, slender tree with a smooth, straight, clear bole of little taper (fig. 2). Young trees have long pyramidal crowns of stout horizontal branches (tilted slightly upwards near the top of the tree) in regular whorls (one produced each year). Occasionally a second flush produces lammas shoots in late summer. Old trees have short, broad, flattened crowns with heavy branches. The rate of branch extension, and hence, crown width, diminishes with age and largely ceases when the canopy closes. The quantity of foliage per tree and branch diameter also decrease with increasing stand density, although foliage weight per unit area increases at close spacings until the canopy closes. In Lake State stands the dry weight of above ground parts was about 20 percent for the crown (about one-third foliage) and 80 percent for the bole. Stump and roots weighed about 20 percent of the above ground portions. Removal of the stump and main root system can greatly reduce the macronutrients on the site, but atmospheric and precipitation nutrient inputs over a rotation can more than offset this removal. The center of gravity was at about one-third the height above the butt *(7,46,76,85, 88,90)*.

Growth and Yield—Cambial growth occurs as springwood cells during the period of active elongation and high auxin synthesis. Summerwood cells are produced following the cessation of terminal growth and consequent reduction in auxin synthesis. The transition from springwood to summerwood varies from season to season in timing and duration and from tree to tree but apparently is associated with seasonal depletion in soil moisture *(76)*.

The amount and distribution of wood growth on the stem are determined largely by crown size and distributions *(51)*.

For the first 50 years height growth on average sites in Minnesota averages about 30 cm (12 in) per year. Between 50 and 100 years the rate is more than 15 cm (6 in) per year. For the next 30 years the rate is only about 7.5 cm (3 in) per year. From 130 to 150 years it drops to 3 cm (1 in). After 150 years height growth almost stops, although diameter growth continues at a slow rate for several years longer. The oldest tree age recorded is 307 years although a tree estimated to be 400 years old was measured on the

Table 1—Characteristics of unmanaged 140-year-old red pine stands on three sites in Minnesota

Item	Site quality Good	 Medium	 Poor
Average d.b.h., cm	39	33	27
Average ht. of dominants, m	32	27	20
Trees/ha	353	460	647
Basal area, m^2/ha	43	41	38
Merchantable yield, m^3/ha			
Total[1]	514	371	248
Lumber[2]	387	244	138
Topwood and small trees	132	126	120
Average d.b.h., in	15.5	13.2	10.7
Average ht. of dominants, ft	104	86	67
Trees/acre	143	186	262
Basal area, ft^2/acre	187	177	164
Merchantable yield			
Total, ft^3/acre[1]	7,350	5,300	3,550
Lumber, fbm/acre[2]	32,500	20,500	11,600
Topwood and small trees, cords/acre	21	20	19

[1] Gross volume, excluding bark, of trees 12.7 cm (5 in) in d.b.h. and larger to a top diameter of 10.2 cm (4 in).

[2] Net volume of trees 20.3 cm (8 in) and larger in d.b.h., to a variable top diameter (minimum 15.2 cm (6 in) inside bark); volumes reduced by 15 percent for woods and mill cull.

Chippewa National Forest in north–central Minnesota.

Normally, mature red pines are about 21 to 24 m (70 to 80 ft) tall, with d.b.h. up to 91 cm (36 in), although trees have attained 46 m (150 ft) in height and 152 cm (60 in) in d.b.h. *(17,76).*

Height growth reflects site quality and the amount of overhead shade or growth disruption, as by terminal feeding insects or other pests; it is greatest on the best sites and least on poor sites or those with a heavy overstory or severe pest damage (table 1). If red pines make up the overstory, the average height of dominant and codominant trees at 50 years (site index) is used to measure site quality. In northern Minnesota the site index ranges from about 14 m (45 ft) for poor sites to 23 m (75 ft) for very good sites *(13,100).* In southeastern Minnesota there are planted stands 26–37 years old with site indices of 27–29 m (90–95 ft) (Donald H. Prettyman, personal communication).

Diameter growth improves with increasing live crown size, which in turn is affected by stand density. The length of live crown in relation to total tree height ranges from 7 percent in dense stands to 75 percent in open stands *(35,50,72,86,90).*

Rooting Habit—During the first summer, seedlings may develop taproots 15 to 46 cm (6 to 18 in) long. Early rooting depth is fostered by the presence of a water table within 1.2 m (4 ft) of the soil surface and a loose soil. Lateral growth usually outstrips vertical growth after the first year. Most root elongation takes place in the spring and early summer with a second spurt in early fall; prevailing soil moisture and temperature conditions influence the timing and intensity of growth *(59,76,90,98).*

The usually well-developed root system in old trees tends to be wide spreading and moderately deep. There are numerous stout lateral roots (and often a taproot) with vertical branches (sinkers) descending at acute angles and often some ascending to within 13 mm (0.5 in) of the surface, giving the tree strong support and making it windfirm. The root system is more extensive on loamy sands than on fine sandy loams.

The lateral roots radiate in an irregular oval shape from the tree at irregular intervals, usually remaining within 10 to 46 cm (4 to 18 in) of the surface and sometimes attaining a length greater than tree height in stands up to 9.4 m (31 ft) tall. They may grow as much as 104 to 130 cm (41 to 51 in) in a year, but usually much less. By 45 to 50 years stem height is twice the length of the longest laterals. Fine roots develop along the main laterals. If unhindered by competition of neighboring trees, the longest laterals may extend 12.2 m (40 ft) beyond the crown limits. In stands, however, the lateral roots are forced to share growing space with root systems of a number of other trees. For example, in an Ontario plantation the roots of a red pine 8.2 m (27 ft) tall extended into the growing space of 23 other trees, and its own space was invaded by the roots of 11 trees.

Both central and lateral vertical roots occur, and these commonly penetrate from 1.5 to 4.6 m (5 to 15 ft) and grow slowly after the first 10 years. Generally the taproot and other vertical roots tend to go through rather than around materials that are difficult to penetrate (in contrast to white pine roots that tend to go around such obstacles).

Red pine roots die back in soils seasonally saturated for more than 3 months and their downward growth is restricted if soil drainage is poor. Hardpan, gley near the surface, coarse compacted soils, and those with bulk densities exceeding 1.40 g/cm^3 (0.81 oz/in^3) stunt root systems *(16,27,76,89,90).*

Mycorrhizae formed on the roots of red pine seedlings by *Boletinus pictus, Tylopilus felleus, Cenococcum graniforme, Gomphidius superiorensis, G. vinicolor,* several species of *Suillus* and *Scleroderma aurantium* improve the uptake of soil moisture and mineral nutrients *(39,67,68,73).*

Natural root grafts, usually 10 to 36 cm (4 to 14 in) below the soil surface, are common in red pines past 15 years old, especially where there is pressure as when two roots grow over or adjacent to a stone. The majority of trees in a stand may be connected directly or in directly with one to six other trees. Grafting is more common among large roots, but occasionally small roots are joined with larger ones. Thinning seems to stimulate an increase in root grafts. Such grafts may transmit diseases (such as *Heterobasidion annosum*), silvicides, and fertilizers but they also retard insect and disease effects on the stumps of cut trees, sustain weak trees during droughts (by transmitting moisture and nutrients), increase windfirmness, and keep girdled trees alive for several years *(32,43,44,76,90,92)*.

Reaction to Competition—Red pine is less shade tolerant than common associates other than jack pine, the aspens, paper birch, and gray birch (*Betula populifolia*). Based on a scale that ranges from 10.0 for eastern hemlock (extremely shade tolerant) to 0.7 for the aspens (extremely shade intolerant), red pine rates 2.4 along with black ash (*Fraxinus nigra*) and black cherry (*Prunus serotina*). Other classifications include red pine in the fourth lowest of five tolerance classes (intolerant). Red pine becomes more intolerant as the environment becomes warmer. Although seedlings may be more tolerant than older trees, they grow very slowly under cover.

Most natural red pine stands are understocked, but an occasional sapling stand may be dense with as many as 49,400 stems per hectare (20,000/acre). Stands 15 to 20 years old with fewer than 6,200 trees per hectare (2,500/acre) seem able to thin themselves, but denser stands stagnate. Dense stands respond well to thinning. To age 67 on an excellent site in Wisconsin, red pine has made full volume growth when thinned periodically from age 32, to an average spacing of 20 percent of height of dominants. Thinning was done after each 2.1 or 2.4 m (7 or 8 ft) of added height growth. Height growth of dominants was retarded after spacing became closer than 15 percent of height. The range of stand density for full volume growth remains to be determined. Although stand density is important in the control of size and quality of timber trees, red pine volume growth varies little over a wide range of stocking conditions (14 to 34 m²/ha or more basal area, or 60 to 150 ft²/acre). On good sites basal area growth ceases when it reaches a level of about 57 m²/ha (250 ft²/acre) *(11,17,22,76,90,101)*.

Diameter growth begins earliest, is fastest, and continues longest in dominant trees. The reverse is true of suppressed trees. Overhead cover restricts height growth, but red pines overtopped by oaks and red maple for as long as 40 years have responded to release.

In dense stands dominance is well expressed by age 10 to 12. At wider spacing the differentiation into crown classes occurs later, usually after 20 or 30 years. In fully stocked stands the percentage of trees in the dominant and codominant crown classes increases from about 45, when average d.b.h. is 5 cm (2 in), to 90, when d.b.h. is 36 cm (14 in). In less dense stands the percentage of dominants and codominants is higher.

Beginning at about age 25 in dense stands, red pine prunes itself better than any other northern conifer except tamarack. Even in dense stands, however, there may be little natural pruning during the first 40 years. In more open stands pruning is delayed to a greater age. On some infertile sands, however, lower branches die off even if crowns are not closed.

In the absence of fire or other catastrophes, the ecological succession in the Lake States is from jack pine to red pine to white pine and finally to northern hardwoods; the rate of succession is likely to be more rapid on the better sites. On the coarser, more infertile sands, succession apparently stops short of the northern hardwood climax and red pine may be a long-persisting subclimax. In much of northern New England and eastern Canada, succession may be to spruce-fir and eastern hemlock. In northeastern Minnesota it may be to spruce-fir alone rather than to northern hardwoods *(66,76)*.

Because the crown is not only the source but also the regulating center for all wood growth, silviculturists can manipulate the stand and some features of site to influence both the quantity and quality of wood desired on various parts of the tree bole. They can thin, prune, fertilize, drain excess moisture, and control insects and diseases to this end under specific circumstances *(51)*.

Because of its shade intolerance, red pine grows best in even-aged groups or stands and is well adapted to even-aged management. Depending on conditions and management objectives either the shelterwood system (fig. 3) or clearcutting followed by planting or seeding may be used. Natural red pine stands in the Lake States commonly are understocked and produce average yields about one-third those produced by well stocked unmanaged stands. Yet even in these understocked stands yields can be increased by about 50 percent with intensive management. For well stocked stands, yields (including intermediate cuts) can be about doubled if managed wisely *(13,14,17,76,101)*.

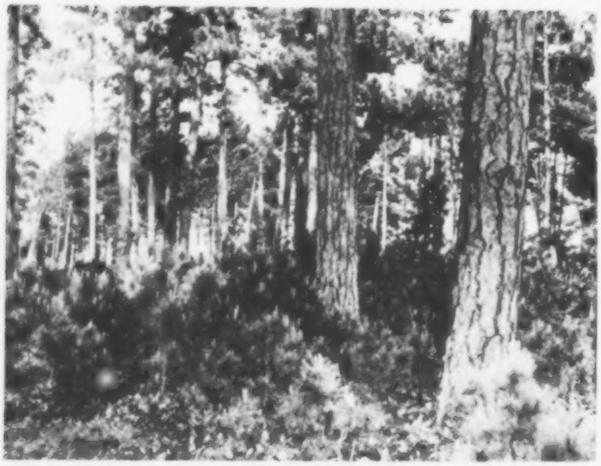

Figure 3—*Abundant red pine reproduction established under a mature red pine stand given frequent light cuts, Chippewa National Forest, north-central Minnesota.*

Damaging Agents—Although red pine has had fewer serious enemies than most associated species when growing under conditions natural to its native range, nevertheless it is damaged by a number of agents. When grown on less acid, finer textured, and more poorly drained soils and under milder climatic conditions than those to which it is adapted, red pine is subject to damage by additional destructive agents.

The following hinder red pine seed germination and early survival: summer drought and high surface soil temperatures; sudden drops in temperature in the early fall, prolonged for about 24 hours, and winter drying of foliage; unidentified insects that consume seedlings shortly after they germinate; competition of subordinate vegetation; postemergent damping-off (usually caused by fungi of the genera *Rhizoctonia, Fusarium, Pythium,* and *Phytophthora),* birds, rodents, flooding, trampling by large animals, and smothering by litter; and large doses of herbicides *(29,76,90,94).*

Beyond the early establishment stage red pine may be killed or seriously damaged by many physical and biotic environmental factors.

Fire may kill red pines in stands up to 21 m (69 ft) tall. Ice and sleet storms and very strong winds have caused serious breakage and windfall in red pine stands. Spray from de-icing salt (sodium chloride) along well traveled highways has caused red pine mortality and poor growth. Spring flooding for 20 days kills red pine *(21,60,76,90,92,93,96).*

About 100 insect species are known to feed on red pine, but only a few usually cause mortality or serious injury. Several sawflies *(Neodiprion lecontei, N. sertifer, N. abbotii, N. nanalus, N. pratti pratti, N. compar, N. pinetum, Diprion frutetorum, D. similis, Acantholyda erythrocephala, A. pini,* and *A. zappei)* defoliate and often kill seedlings, and some of them damage older trees also. Trees in young stands, especially plantations, may sustain mortality or serious injury from the Saratoga spittlebug *(Aphrophora saratogensis),* the Zimmerman pine moth *(Dioryctria zimmermani),* the red pine shoot moth *(D. resinosella)* or the Allegheny mound ant *(Formica exsectoides).* The red pine scale *(Matsucoccus resinosae),* especially in the Northeast, kills or severely injures red pines from seedlings to mature trees. The European pine shoot moth *(Rhyaciona buoliana)* frequently deforms young red pine. White grubs (such as *Phyllophaga rugosa, P. tristis, Diplotaxis sordida,* and *Serica* spp.) cut the roots of the seedlings and often induce mortality in dry years *(10,34,75,76,102).*

In periods of peak population, the snowshoe hare and the cottontail often kill or reduce height growth of red pine seedlings. When preferred foods are lacking, white-tailed deer browse or destroy red pine seedlings. Porcupines girdle red pines from sapling to mature trees *(9,76).*

The North American strain of scleroderris canker *(Gremmeniella abietina)* has caused the loss of a number of young plantations in the Lake States; in the Northeast, the European strain of scleroderris canker has killed mature red pine. Needle cast diseases can retard growth of red pine and kill small trees. These include *Lophodermium pinastri* and *Scirrhia acicola*. Sirococcus tip blight *(Sirococcus strobilinus)* can cause failure of natural regeneration when overstory trees are infected. *Coleosporium asterum* stunts the growth of new shoots while sweetfern blister rust *(Cronartium comptoniae)* deforms young trees. In nurseries, *Cylindrocladium scoparium* occasionally causes severe losses through root rot, damping off; and needle blight, and annosus root rot *(Heterobasidion annosum)* and the shoestring root rot *(Armillaria mellea)* cause death of trees in planted and natural stands *(7,39,63,65,68,76,82, 83,90).*

Special Uses

Red pine has been grown primarily for the production of wood for lumber, piling, poles, cabin logs, railway ties, posts, mine timbers, box boards, pulpwood, and fuel. It has been one of the most extensively planted species in the northern United States and Canada, not only for wood production but also for dune and sandblow control, snowbreaks, windbreaks, and Christmas trees. Even when wood production is the main goal, red pine forests often are managed throughout their rotation for other uses such as recreation, wildlife habitat, and watersheds.

On sandy farmland in the Lake States, narrow strips (usually 3 to 8 rows) of red pine have been planted at intervals to reduce wind-caused soil erosion in the fields. Similarly, narrow strips have been planted along roads to control snow drifting and to improve scenic aspects. Red pine has been planted to help control sand dunes near Lake Michigan and also to control "sandblows" that develop when cover is removed from light sandy soils. Such stands should be managed to retain long live crowns and to maintain good vigor without losing essential reduction of wind velocities.

Red pine stands are popular places for hiking, camping, and other recreational activities, especially when the trees are large and located near a lake or stream. Red pine forests used for recreation should be managed to maintain a high proportion of large old-growth trees.

Red pine stands produce litter (more than 9000 kg/ha or 8,000 lb/acre at age 15) that helps prevent erosion by absorbing moisture, but they also contribute to moisture depletion in the top 1 m (3.3 ft) of soil. Such stands also increase the snowpack water content and consequently the spring snowmelt runoff over that of unplanted areas or those growing deciduous trees. The water yield of red pine stands in Minnesota was less than for aspen stands and decreased with stand density. Well stocked young red pine stands intercept some precipitation (average throughfall is 87 percent and stem flow 2 percent of precipitation).

The management of red pine stands should be coordinated with that of other types on a watershed so as to deter soil erosion and maintain an even flow of high quality water.

Although red pine stands generally are considered poor habitat for game birds and animals, they provide cover, nesting sites, and some food for many species of birds and animals. For wildlife purposes the stands should be managed in patches so as to provide an array of conditions from small openings to mature groups *(13,14,15,18,38,77,78,79,80,97)*.

Genetics

Red pine is uniform morphologically and apparently very old. Fossil records from Dakota sandstone show that an upland pine *(Pinus clementsii* or *P. resinosipites* or both) markedly resembling red pine occurred in southern Minnesota during the Cretaceous period. During periods of glaciation, red pine was forced to migrate to the south and then returned north with the retreat of the glaciers. Indications are that after the most recent glaciation red pine migrated west, principally north of Lake Michigan, from a refuge in the Appalachian Highlands *(76,103)*.

Population Differences

Although appreciable natural variation between red pine stands within a region has been noted, it appears to reflect largely nongenetic environmental effects. Actually, variation in progeny means from individual trees can be as great as, or greater than, that between population or provenance means. Conclusions from an Ontario study were that the variation pattern of red pine was predominantly random from stand to stand. In a Wisconsin study, family differences contributed the bulk of the variation observed with differences among stands and seed collection regions contributing little.

Despite the unusual uniformity of the species, occasional red pines have been found with fastigiate branching, unusually slender branches, markedly suppressed lateral branching, or dwarf habit. Very small occurrences of albino or chlorophyll-deficient mutant seedlings, and tetraploid seedlings have been reported. Red pine shows only minor inbreeding depression following selfing—an indication that it carries few deleterious mutant genes. In Ontario individual open grown red pine trees showed differences in susceptibility to attack by *Neodiprion lecontei (1,28,33,40,42,76)*.

Races

Seed source studies have disclosed small, but statistically significant differences among provenance means for survival, phenological traits, size and growth rates, photoperiodic response, lammas frequency, and wood quality. For plantations up to age 20, the difference between the overall mean and the mean of the best provenance has been about 10 percent for height growth. Very young seedlings have shown greater differences and older trees less. Red pine from the Angus, ON, area has shown enough promise to be used for establishing seed orchards in Ontario and adjacent areas.

Some effects of climate noted for red pine indicate that northern sources may have smaller seeds, seedlings with fewer cotyledons, lower frequency of lammas growth, and less frost sensitivity. Provenances from different climatic regions have shown differences in height growth and several other attributes, but variation between provenances within climatic regions is also present. In general, red pine traits show broad regional adaptation and broad regional differences as well as random occurrence *(28,41, 42,84)*.

Hybrids

No authenticated interspecific hybrids involving red pine have been found in nature. A *Pinus nigra* var. *austriaca* × *P. resinosa* cross previously reported no longer is considered a valid red pine hybrid. Many additional hybridization attempts in the United States and Canada have failed, although one cross with Austrian pine and one with Japanese red pine *(Pinus densiflora)* using highly irradiated (200 000 R) red pine pollen have been reported from Ontario. One tree of each cross survived at age 10. The trees were about 1 m (3 to 4 ft) tall, and each showed some hybrid characteristics *(105)*.

The growth rate of hybrids between provenances was intermediate between those of the parent provenances and showed no evidence of heterosis.

The best opportunity for genetically improving red pine, therefore, is to incorporate small genetic gains in large numbers of seedlings when red pine is a major part of large-scale reforestation programs *(28,42,47,62,90,104)*.

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Pinus rigida Mill. Pitch Pine

Pinaceae Pine family

Silas Little and Peter W. Garrett

The species name of pitch pine (*Pinus rigida*) means rigid or stiff and refers to both the cone scales (*17*) and the wide-spreading, sharply pointed needles (*5*). It is a medium-sized tree with moderately strong, coarse-grained, resinous wood that is used primarily for rough construction and where decay resistance is important. One tree in Maine measured 109 cm (43 in) in d.b.h., 29 m (96 ft) tall, with a crown spread of 15 m (50 ft) (*11*).

Habitat

Native Range

Pitch pine (fig. 1) grows over a wide geographical range—from central Maine to New York and extreme southeastern Ontario, south to Virginia and southern Ohio, and in the mountains to eastern Tennessee, northern Georgia, and western South Carolina. Be-

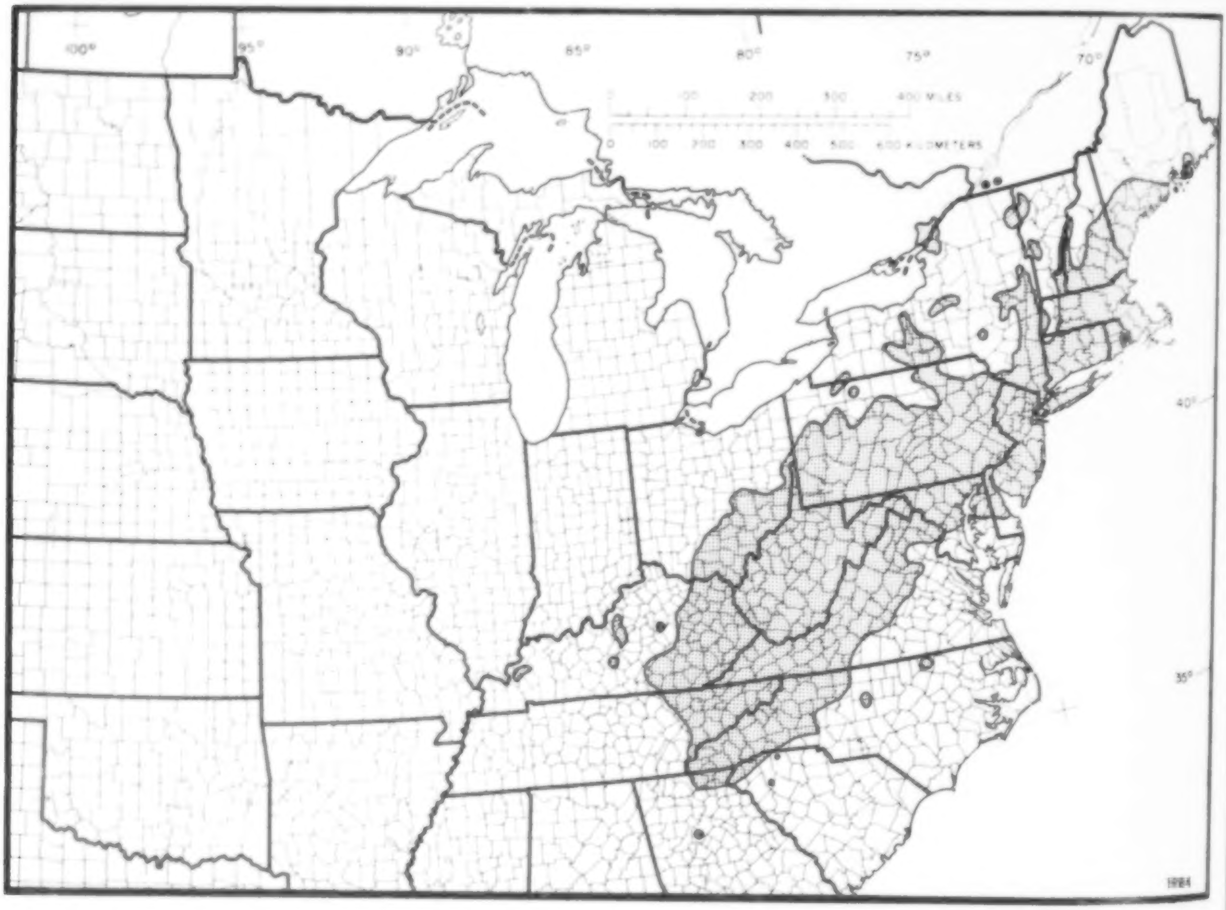

Figure 1—*The native range of pitch pine.*

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cause it grows mostly on the poorer soils, its distribution is spotty.

In the Northeast, pitch pine is most common on the sandy soils of Cape Cod, Long Island, and southeastern New Jersey, and in some sections of sandy or shallow soils in Pennsylvania *(19)*.

Climate

The climate in the range of pitch pine is humid. Average annual precipitation is usually between 940 and 1420 mm (37 and 56 in) and is well distributed throughout the year. Length of the frost-free season ranges from 112 to 190 days and temperatures range from winter lows of -40° C (-40° F) in the northern part of the range to summer highs of more than 38° C (100° F) in most sections *(9)*.

Soils and Topography

Pitch pine is usually restricted to the less fertile soils—those of shallow depth, or of sandy or gravelly texture. Many of the northern stands are found on sandy outwash plains of glacial origin. The species also occupies sandy and gravelly soils of alluvial and marine origin. In the highlands of northern New Jersey, southern New York, Pennsylvania, and south through the mountains, it is most common on steep slopes, ridges, and plateaus where the soils are shallow.

Generally, pitch pine grows on Spodosols, Alfisols, Entisols, and Utisols. In southern New Jersey, the pH of the A and B horizons range from 3.5 to 5.1, and in northern New Jersey, from 4 to 4.5 *(9)*.

Pitch pine grows on sites with a wide range of moisture conditions. In southern New Jersey it is found on excessively drained, imperfectly drained, and poorly drained sands and gravels, as well as on muck soils in the white-cedar swamps. Even in the hilly regions it grows on both well drained and excessively drained slopes and in the swamps *(9)*.

In New England it is most common in the coastal districts and in river valleys. In New York it is not common above 610 m (2,000 ft), but in Pennsylvania it grows at all elevations up to the highest point in the State, 979 m (3,213 ft) *(13)*. In the Great Smoky Mountains and vicinity, pitch pine is found at elevations between 430 and 1370 m (1,400 and 4,500 ft). In hilly sections, pitch pine often occupies the warmer and drier sites, those facing south or west *(9)*.

Associated Forest Cover

Pitch pine is the major component of the forest cover type Pitch Pine (Society of American Foresters Type 45) and is listed as an associate in nine other types *(8)*: Eastern White Pine (Type 21), Bear Oak (Type 43), Chestnut Oak (Type 44), White Pine-Chestnut Oak (Type 51), White Oak-Black Oak-Northern Red Oak (Type 52), Shortleaf Pine (Type 75), Virginia Pine-Oak (Type 78), Virginia Pine (Type 79), and Atlantic White-Cedar (Type 97). In addition to the species named in the types, pitch pine associates are Table Mountain pine *(Pinus pungens)*, gray birch *(Betula populifolia)*, post oak *(Quercus stellata)*, blackjack oak *(Q. marilandica)*, scarlet oak *(Q. coccinea)*, southern red oak *(Q. falcata)*, various hickories *(Carya* spp.), blackgum *(Nyssa sylvatica)*, red maple *(Acer rubrum)*, and eastern hemlock *(Tsuga canadensis)*.

According to the Forest Survey, pitch pine types cover 9 900 ha (24,500 acres) in New Hampshire, 85 400 ha (211,000 acres) in Massachusetts, 1200 ha (3,000 acres) in Rhode Island, possibly 44 500 ha (110,000 acres) in New York, more than 121 400 ha (300,000 acres) in Pennsylvania, and more than 283 300 ha (700,000 acres) in New Jersey. Other Northeastern States contain fewer hectares of this species, though about 187 400 ha (463,000 acres) in Maryland and 346 000 ha (855,000 acres) in West Virginia were classified in the Forest Survey as having pitch pine-Virginia pine-hardwood stands. However, in these two States, the Virginia pine *(Pinus virginiana)* component greatly exceeds pitch pine in most stands *(9)*.

Usually, the most common shrubs growing with pitch pine on upland sites are lowbush blueberries (often *Vaccinium vacillans* or *V. angustifolium*) and black huckleberry and dangleberry *(Gaylussacia baccata* and *G. frondosa)*. Some stands include bear oak *(Quercus ilicifolia)*, dwarf chinkapin oak *(Q. prinoides)*, and mountain-laurel *(Kalmia latifolia)*.

Lowland sites where pitch pine predominates have a variety of shrubs. Common ones include sheep-laurel *(Kalmia angustifolia)*, leatherleaf *(Chamaedaphne calyculata)*, staggerbush *(Lyonia mariana)*, inkberry *(Ilex glabra)*, dangleberry, highbush blueberry *(Vaccinium corymbosum)*, and swamp-honeysuckle *(Rhododendron viscosum)* *(9)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pitch pine is monoecious; pistillate flowers often occur on higher branches than the staminate flowers, but some shoots may have both types of flowers. The pistillate flowers grow in one cluster and less commonly in two clusters on a shoot, the latter as a result of polycyclic winter buds *(15)*. Staminate flowers are yellowish, sometimes purplish, when mature, and 13 to 25 cm (about 0.5 to 1 in) long. The mature pistillate flowers are green but often show some red. They are borne on stout stalks and are 8 mm (0.33 in) long without the stalk, 20 mm (0.8 in) with the stalk. In southern New Jersey, the staminate flowers of pitch pine are visible by the third week of April; pistillate flowers usually by May 1. Pollen shedding usually occurs during the second or third week of May *(9)*.

Cones reach full size, 4 to 7 cm (1.5 to 2.8 in) long, and mature at the end of the second summer. Mature cones are 2.5 to 3.5 cm (1.0 to 1.4 in) wide when closed, 4.5 to 5.5 cm (1.8 to 2.2 in) wide when open. Closed cones are narrowly ovoid; open cones are ovoid and flattened at the base.

Seed Production and Dissemination—Vigorous open-grown basal sprouts start bearing mature cones when only 3 years old. Of 400 planted 2-year-old seedlings, two bore a total of three mature cones at the end of their second growing season in the plantation *(2)*. Potted seedlings may be even more precocious, occasionally bearing female flowers in 12 months. However, mature cones are not usually borne on open-grown trees until they are 8 to 12 years old. Shade-grown trees produce cones at a later date *(19)*.

Although pitch pine is reported to bear good crops of cones at approximately 3-year intervals, production may be irregular. In southern New Jersey, good to excellent crops have occurred at intervals of 4 to 9 years. Occasionally, poor crops are borne in two successive years, although usually a poor crop is followed by fair to excellent crops for 1 to 3 years *(9)*.

Pitch pine seeds are three-angled and 4 to 5 mm (0.16 to 0.20 in) long, although with the wings they are 15 to 21 mm (0.6 to 0.8 in) long. Because they differ in size, the number of seeds per unit of weight varies widely— from 97,700 to 181,200/kg (42,500 to 82,200/lb). In nursery practice fresh seeds need no stratification before sowing, and seeds are merely pressed in the soil at rates that produce 320 to 380 seedlings/m^2 (30 to 35/ft^2) *(27)*. While northern nurseries usually leave the seedlings in the seed bed for 2 years, southern nurseries lift year-old seedlings for planting.

Seed dissemination is variable, depending on the length of time that cones remain closed after maturity. On some trees, the cones open soon after maturity; at the other extreme, some cones remain closed for many years, until the heat of a fire opens them or until the trees are cut. Trees of the latter type are characteristic of the areas with a long history of wildfire.

Cone behavior is thought to be an inherited characteristic, but in southern New Jersey, groups of trees with different cone behavior are not widely separated geographically.

When cones open soon after maturity, seed dispersal begins about November 1 and ends in April in southern New Jersey *(18)*. The pattern of dispersal seems similar to the pattern for shortleaf pine (*Pinus echinata*); in one study this species dropped 69 percent of its seed the first month, and 90 percent during the first 2 months. In New Jersey, probably about 90 percent of the seeds dispersed from a pitch pine source fall on the east side because the prevailing fair-weather winds are from the west *(9)*.

On trees showing cone behavior between the two extremes, the cones open erratically within a few years after maturity. Apparently there is no fixed pattern of when, what, or how many cones open.

Although equipped with large wings, pitch pine seeds usually are not carried very far by wind. On the leeward of one stand, all natural reproduction in an abandoned field was within 90 m (300 ft) *(9)*.

Seedling Development—Although it was reported that seeds from trees less than 8 years old are usually sterile, other data do not support the generalization. In a cutting test on 200 seeds from 3-year-old sprouts, 94 percent were sound. In another study, 52 percent of the seeds in two cones from 4-year-old seedlings germinated within 9 days *(9)*.

Some pitch pine seeds may remain viable in the forest floor for 1 year, but there is no evidence that they can lie over for longer periods. In one instance, after heat from a July wildfire had opened many closed cones, most of the seeds germinated the following spring, though a few lay dormant until August and germinated after rains had broken a severe dry period. In another instance, when 2,400 seed spots were sown to pitch pine in late March 1955, delayed germination in the spring of 1956 provided as many as 1.4 seedlings per spot in some treatments *(9)*. Germination of pitch pine seeds is epigeal *(27)*.

Thick litter is unsuitable as a seedbed, even on poorly drained sites. In one study few seedlings were found in July on the thick litter of unburned sites. On similar areas treated with a severe September fire before seedfall, 16,600 to 56,300 seedlings per hectare (6,700 to 22,800/acre) were tallied on very poorly to imperfectly drained sites, and 2,200/ha (900/acre) on upland sites *(21)*.

Droughts kill many pitch pine seedlings, but those less than 2 years old are most susceptible. A summer drought in 1957 killed 81 percent of the seedlings from a 1956 direct seeding in certain plots, and on comparable sites most of the seedlings started in 1955 survived *(9)*.

At the end of the first year, shaded seedlings on upland sites usually have a height of about 2.5 cm (1 in), and a taproot 8 to 10 cm (3 to 4 in) long with a few laterals. In contrast, vigorous open-grown 1-year-old seedlings on upland sites may have stems 5 to 10 cm (2 to 4 in) high with a maximum height of 13 cm (5 in) and correspondingly greater root systems. On the moister, poorly drained sites, open-grown first year stems are usually 8 to 15 cm (3 to 6 in) high with a maximum height of 20 cm (8 in).

Pitch pine seedlings grow slowly for the first 3 to 5 years and then more rapidly. Some planted stands in Pennsylvania maintained an average height growth of 36 to 48 cm (14 to 19 in) between ages 6 and 17. After a seed-tree cutting in a New Jersey stand, the average height growth of dominant seedlings among the natural pitch pine reproduction was 0.5 and 0.7 m (1.5 and 2.2 ft) during the third and fourth growing seasons after the cutting, respectively *(9)*.

Deer browsing and hardwood competition both reduce pine growth rates. In one study, young pines uninjured by deer grew 0.6 to 1.2 m (2 to 4 ft) more during a 5-year period than those that had their leaders browsed two or more times. In another study, cutting back hardwood sprouts twice resulted, after 6 years, in a 1.2 m (4 ft) increase in the height growth of the largest pines *(9)*.

Vegetative Reproduction—Among eastern conifers, pitch pine has an outstanding ability to survive injury. Even if all the foliage is killed by the heat of a fire, the crown can "green up." If 0.6 to 0.9 m (2 to 3 ft) of the terminal shoot is killed, a new one may develop. If the entire stem is killed, sprouts frequently start at the base *(19,25)*. Deer may clip a seedling back to 3 or 5 cm (1 or 2 in) above the ground, and still it may live *(9)*.

Dormant buds capable of active growth when properly stimulated are the key to this recovery. Also, the thick bark gives a relatively high degree of protection to the dormant buds and to the cambium. Both pitch and shortleaf pines have these buds along the bole to an age of 60 years or more, but at such ages only in pitch pine do the buds at the base retain the potential for growth. In seedlings that have not yet developed thick bark, the lowermost buds may be protected by characteristic basal crooks in the stem that bring them into or against mineral soil on upland sites. Such buds often survive fires and produce new shoots *(22,29,30)*.

Pitch pine seedlings that cannot sprout after fires are those occasional seedlings that never develop a basal crook, and around which insufficient soil accumulates to protect the buds; those that started on sphagnum or on the deep humus layer of poorly drained sites, and around which fire burns deeper than the surface where they became established; and those too young to have well-developed basal crooks. Though some open-grown seedlings may develop such crooks in their first year, shade-grown seedlings may take 9 to 10 years *(20,22)*.

The sprouting vigor of older pitch pines varies with their life history. When single stems more than 40 years old are cut, some sprouts start but most die within 2 years. In contrast are the multistemmed stools that characterize some southern New Jersey localities with a history of frequent wildfires; these stools may be 60 to 90 years old and commonly have produced several generations of sprouts. The survival of new sprouts on such old stools may be associated with partial rejuvenation of the root systems *(9)*.

Although pitch pine's sprouting ability is an asset in enabling trees to survive fire or other injuries, it is also a liability from the commercial point of view. Apparently the form and growth rate of sprouts decrease markedly with increased age of the root crown after crown age reaches about 20 years. Where wildfires have occurred at frequent intervals, often stands are composed largely of slow-growing sprouts from old stools. In many other stands the stems have been deformed by past fires and manifest boles with many small branches that have developed to replace killed crowns, boles with one or more crooks or forks where terminal shoots have been killed, or trees with flat tops where no leader has developed after the last one was killed.

Sapling and Pole Stages to Maturity

Growth and Yield—Pitch pine (fig. 2) reaches a maximum age of 200 years and a maximum height of 30 m (100 ft) in Pennsylvania *(13)*. Individual trees exceeding 350 years of age have been reported in southeastern New York. In stands it is seldom more than 24 m (80 ft) tall or 61 cm (24 in) in d.b.h.

On the better sites in Pennsylvania, pitch pine maintains an average annual height growth of 0.3 m (1 ft) or more until the trees are 50 to 60 years old. The rate of height growth then starts to decline, and the trees add little to their height after they are 90 to 100 years old. On the best sites, diameter growth

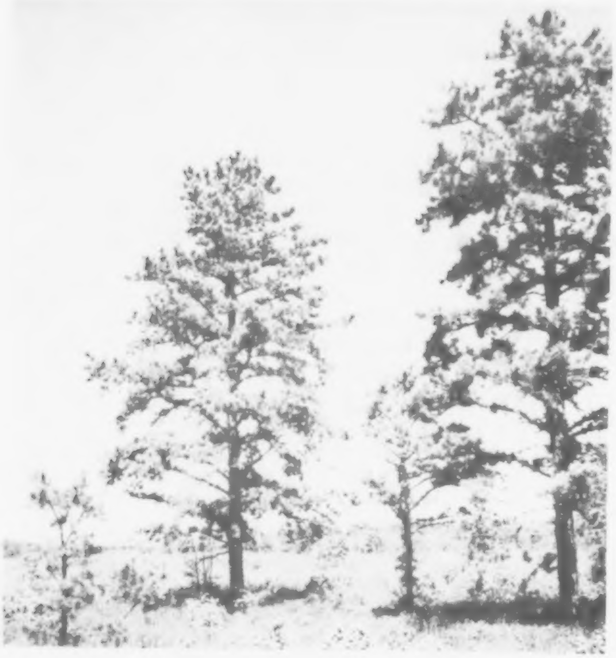

Figure 2—*Open-grown pitch pine in Berkshire County, MA.*

is 2.5 cm (1 in) in 5 years at 20 years of age, and falls to 2.5 cm (1 in) in 8 years at 90 years *(9)*.

Total volume in cubic meters is maximum in Pennsylvania at 90 years, when fully stocked even-aged stands yield 210 to 350 m^3/ha (15,000 to 25,000 fbm/acre). However, mean annual growth reaches its maximum at about 30 years—3.0 to 5.8 m^3/ha (43 to 83 ft^3/acre), depending on the site *(9)*.

In closed stands of seedling origin undamaged by fire, pitch pine self-prunes about as well as shortleaf pine, but in understocked stands it tends to produce somewhat larger and more persistent branches than shortleaf. Open-grown trees typically develop large spreading branches, which contribute to the rough appearance that many people associate with the species. Typical pitch pine stands have been burned repeatedly, are understocked, and have suffered fire injury; consequently trees have either retained branches or have developed them from dormant buds along the boles.

Even without the stimulus of fire, pitch pines suddenly released by heavy cutting in a stand may develop branches along the bole. Pruning of living branches also may stimulate the development of new branches from buds or short shoots *(9)*.

Rooting Habit—Root development of the older pitch pines varies with the site. On sandy, well-drained soils, trees 10 cm (4 in) and larger in d.b.h. may have vertical roots that reach depths of 2.4 to 2.7 m (8 to 9 ft), but on heavier or wetter soils the root systems are more shallow. However, even in saturated soils where water tables are less than 0.3 m (1 ft) below the surface, pitch pine roots may reach depths of 0.9 to 1.5 m (3 to 5 ft) on sandy sites. There, and in the swamps, pitch pine roots live and grow below the water table, and mycorrhizae occur on some of the submerged roots *(9,22)*.

Possibly because pitch pine roots so deeply, it is relatively windfirm. In Maryland, Virginia pine proved much more susceptible to windthrow than pitch pine *(9)*.

Reaction to Competition—Pitch pine is intolerant of shade. On swamp sites, it is less tolerant than Atlantic white-cedar *(Chamaecyparis thyoides)*, and on poorly drained or upland sites it is less tolerant than its common hardwood associates—blackgum, red maple, various oaks, and hickories *(9)*.

In view of its relatively low tolerance and its requirement of mineral soil for germination, pitch pine can best be maintained in stands by even-aged management with seedbed preparation and control of competing hardwoods.

Fire has been largely responsible for maintaining the pitch pine type and also has been responsible for the sprout origin, comparatively slow growth, and poor form that characterize this species. One severe fire may eliminate nonsprouting associates such as white pine *(Pinus strobus)*; repeated severe fires may eliminate such species as shortleaf pine *(P. echinata)* and white oak *(Quercus alba)* which do not produce seed at as early an age as pitch pine and bear oak.

Damaging Agents—Deer, rabbits, mice, wind, snow, ice, and salt spray damage pitch pine stands. Damage by deer and rabbits is limited to small seedlings or sprouts. The most common wind damage is breakage of defective large trees. However, severe storms, such as hurricanes, also may cause much windfall damage in the oldest natural stands and in plantations more than 20 years old, especially if the planted trees are infected with root rots. Heavy wet snows or ice occasionally break leaders or branches in trees of all sizes, but open-grown stems with large branches, particularly those 2.4 to 4.6 m (8 to 15 ft) tall, seem most susceptible. Although pitch pine foliage is more resistant to salt-spray damage than that of associated species, hurricanes or gales can deposit sufficient spray to injure or kill its foliage over extensive coastal areas. Few affected pitch pines die however; the chief result is reduction in growth *(4,23,27)*.

Several fungi that attack pitch pine but usually do not cause serious or extensive damage are stem rusts such as *Cronartium comptoniae, C. quercuum, C. quercuum* f. sp. *fusiforme*, and *C. comandrae (1)*; several needle rusts and blights such as nine species of *Coleosporium, Ploioderma lethale*, and *P. hedgcockii*; twig cankers such as *Diplodia pinea*; root rots such as *Heterobasidion annosum*; and trunk rots, chiefly *Phellinus pini*. Heart rot as a result of *P. pini* does not become important in stands until the trees are 75 years old *(3,12)*.

Many insects attack pitch pine *(6)*. The most important are the tip moths *(Rhyacionia frustrana* and *R. rigidana)*, the pitch pine looper *(Lambdina athasaria pellucidaria)*, the sawflies (chiefly *Neodiprion lecontei, N. pratti paradoxicus*, and *N. pinusrigidae)*, the southern pine beetle *(Dendroctonus frontalis)*, the pine webworm *(Tetralopha robustella)*, and the pine needleminer *(Exoteleia pinifoliella)*. Loopers periodically cause extensive damage to pitch pine in Massachusetts; in 1954 they defoliated pines on more than 20 230 ha (50,000 acres) of Cape Cod *(9)*.

Special Uses

Pitch pine was an important tree during the days of wooden ships and iron men. Its coarse-grained wood is only moderately strong but contains a comparatively large amount of resin, weighing about 513 kg/m^3 (32 lb/ft^3). Consequently, the wood resists decay, which makes it particularly useful for ship building and for rough construction, mine props, fencing, and railroad ties. It is also used for pulpwood, crating, and fuel. At one time the wood was destructively distilled for naval stores *(5,7)*.

Pitch pine also serves as a food source for wildlife. Cones of pitch pine often remain on the trees unopened for several years or until the heat from a forest fire opens them. Seeds shed in mid-winter are an important source of food for squirrels, quail, and small birds such as the pine warbler, pine grosbeak, and black-capped chickadee. White-tailed deer and rabbits also browse young sprouts and seedlings *(5,7)*.

Genetics

Based on isozyme analysis, only a small percentage of genetic diversity in pitch pine appears to be due to seed source. Most variation appears to be due to differences between individuals within populations. The dwarf populations of the New Jersey Pine Plains are essentially indentical in genic constitution to tall trees of the Pine Barrens, at least for the allozyme loci sampled. Whatever factors are responsible for the dwarf size of these populations, they have not resulted in detectable changes in allozyme frequencies among populations *(10)*.

Provenance/progeny tests of 156 trees in 17 natural stands of pitch pine distributed over the Atlantic coastal plain from Cape Cod, Massachusetts, to Cape May, New Jersey, were established in central New Jersey. Trees from southern seed sources grew faster than those from northern seed sources but adaptation of all sources decreased with increasing distance from the seed source. Variation among families within these 17 provenances was negligible *(14)*.

There is an apparent contradiction between growth in provenance/progeny trials and isozyme analysis in different populations of pitch pine in central New Jersey *(10)*. The isozyme studies seem to indicate that variation is due to differences between individuals, while the provenance/progeny trials suggest that variation in this species is due to seed source and not differences among families within a provenance. Whether to select provenances or individuals within provenances for tree improvement programs therefore is still an open question.

The differing cone-opening characteristics discussed earlier seem to be inherited, and trees at each extreme perhaps should be considered as separate races or ecotypes.

When pitch and shortleaf pines grow together, natural crossing may occasionally occur. Trees with intermediate characteristics have been seen in southern New Jersey, and similar trees have been reported in southern Pennsylvania *(9)*.

At Placerville, CA, the Pacific Southwest Forest and Range Experiment Station crossed pitch pine with shortleaf, pond, Table Mountain, and loblolly pines. Pitch × loblolly hybrids *(P. × rigitaeda)* are produced in large quantities in South Korea for commercial plantings. Early field trials in Illinois, Maryland, and New Jersey showed only slight promise *(9)*. With more careful selection of parent trees and extensive screening trials, the Northeastern Forest Experiment Station produced hybrids with exceptionally fast growth, good form, and winter hardiness for much of the natural range of pitch pine *(20,21)*.

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Pinus sabiniana Dougl. **Digger Pine**

Pinaceae **Pine family**

Robert F. Powers

Digger pine (*Pinus sabiniana*), also called bull pine or gray pine, has limited commercial use today, but it once was important to California Indians, who used its seeds and parts of cones, bark, and buds as food supplements, and its twigs, needles, cones, and resin in basket and drum construction *(23,30)*. Indians and early settlers used the resin of Digger pine for medicinal purposes. During California's gold rush period, from 1848 to 1860, all foothill timber, including Digger pine, was heavily used for fuel and structural materials. Despite these uses, Digger pine was viewed with contempt by many early settlers who placed slight value on a tree that provided little shade and poor lumber. In fact, the term "Digger" stems from a contemptuous name given by early settlers to the many small Indian tribes once occupying central California.

Habitat

Native Range

A California endemic, Digger pine (fig. 1) grows between latitude 34° 30′ and 41° 15′ N. Generally found between elevations of 300 to 900 m (1,000 to 3,000 ft) in dry foothill woodland communities of California's Central Valley, natural stands of Digger pine also grow from as low as 30 m (100 ft) at several locations on the floor of the Sacramento Valley to almost 2130 m (7,000 ft) near Sawtooth Peak in Inyo County *(10)*. Digger pine is found in the Coast and Cascade Ranges, Klamath Mountains, southwestern Modoc Plateau, western Sierra Nevada, and Tehachapi Mountains, and over a broad environmental sweep, from the westerly edge of the Mojave Desert, to the Santa Lucia Mountains in Monterey County within sight of the Pacific surf *(6)*. Digger pine is absent in a conspicuous 89-km (55-mi) gap near its southern Sierra Nevada limit. The cause of the gap is unknown but was noted as early as 1865 *(10)*.

Climate

Temperatures characterizing Digger pine's range span the gamut of coastal to Great Basin climates. Yearly means vary from 10° to 17° C (50° to 62° F), with mean minima of –2° to 3° C (28° to 37° F), in the coolest months, and mean maxima of 31° to 36° C (88° to 97° F) in the warmest months *(30)*. Individual summer days often exceed 38° C (100° F). Few tree species grow over as wide a range in precipitation as Digger pine, with annual averages varying from 250 mm (10 in) at the edge of the Mojave Desert to 1780 mm (70 in) at its upper limits in the Sierra Nevada *(6)*. Sites receiving as little as 80 mm (3 in) of precipitation in a single season continue to support stable populations *(30)*.

Despite the apparent diversity in climatic tolerance shown by Digger pine, four climatic conditions characterize most of its natural range: hot, dry summers; absence of summer fog; precipitation, mostly as rain; and generally mild winters. Digger pine's ability to withstand summer drought and to photosynthesize during mild periods of winter and spring give it a strong competitive advantage over many other species in the California foothills.

Soils and Topography

Digger pine grows on soils in five soil orders (Alfisol, Entisols, Inceptisols, Mollisols, and Ultisols) derived from a wide variety of geologic materials including granodiorite, dacite, andesite, basalt, peridotite, greenstone, schists of various types, limestone, river gravels, and sandstone. The striking feature in much of Digger pine's range is its association with ultramafic soils, particularly those formed from serpentinite. Inclusions of serpentinite or limestone in upland zonal soils produce nutritional imbalances that allow Digger pine to persist within the mixed-conifer forest of the Sierra Nevada and the conifer-hardwood forest of the north Coast Ranges (fig. 2) *(6)*.

Soils supporting stable populations of Digger pine characteristically have low levels of available moisture. Even on sites where soil moisture is relatively high, Digger pine tends to dominate only the shallowest phases. Although found on deep, alluvial valley terraces, Digger pine has been eliminated systematically from many fertile sites by stockmen seeking to increase grass production *(6,18,30)*. Today, many of the sites still supporting Digger pine consist of dry rolling hills, rocky slopes, and steep canyon walls (fig. 3). Few conifer species can match Digger pine's ability to persist under such xeric, sterile conditions.

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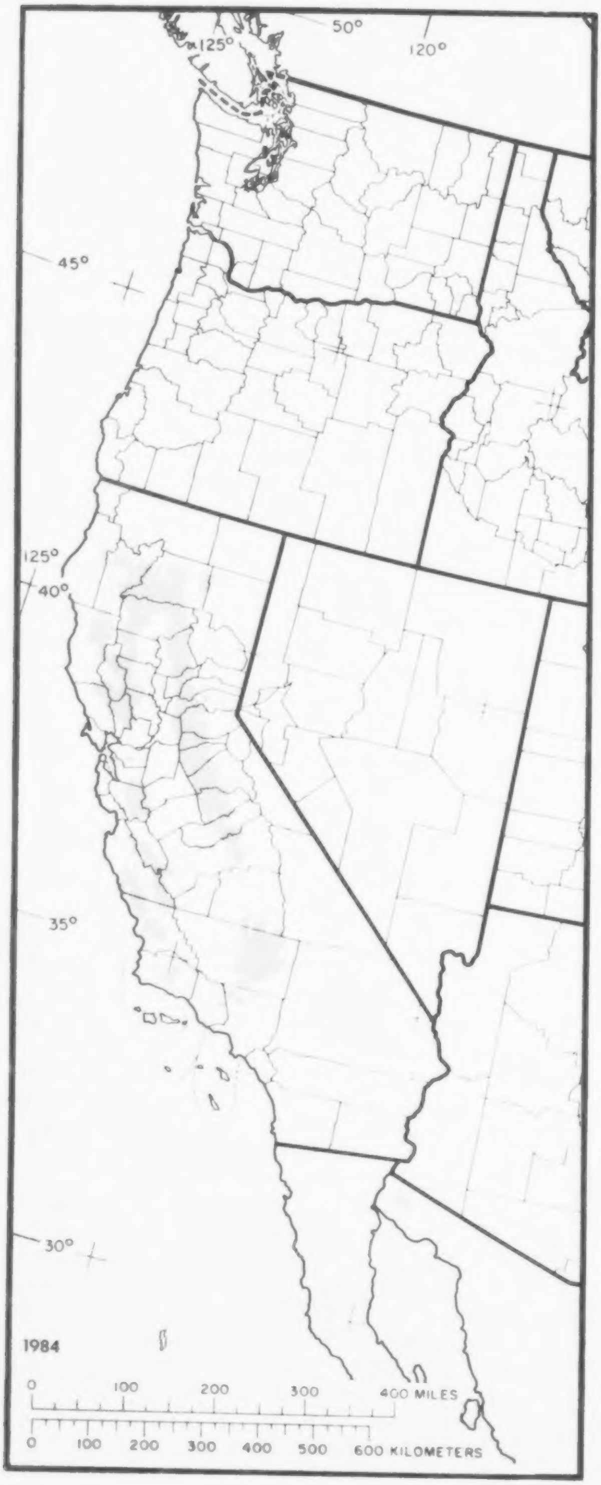
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Figure 1—*The native range of Digger pine.*

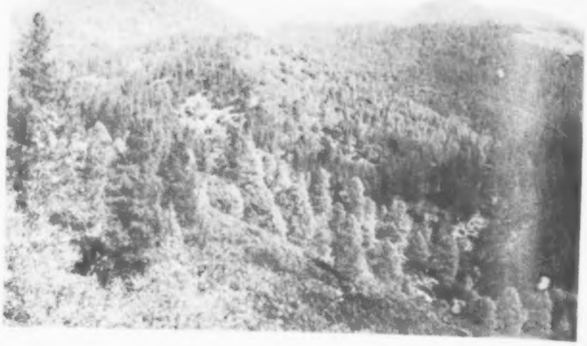

Figure 2—*Nutritionally imbalanced soils allow Digger pine to extend into other forest types. Here, exposed limestone supports a stand of Digger pine in a forest of Pacific Ponderosa Pine—Douglas-Fir (SAF Type 244).*

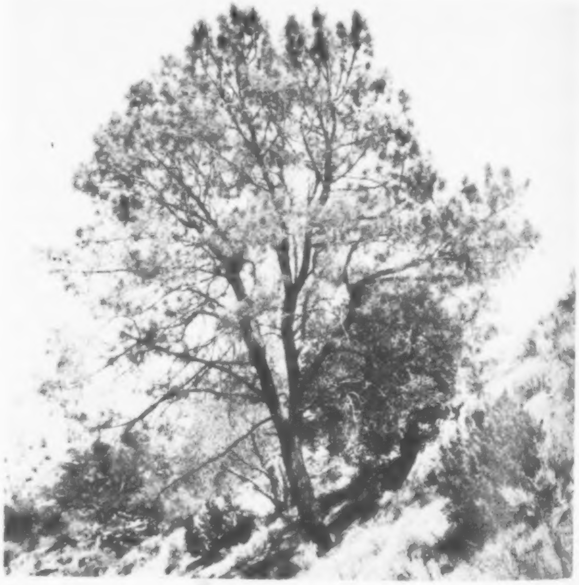

Figure 3—*Digger pine is common to the foothills of the Sierras.*

Associated Forest Cover

Digger pine forms a part of variants of seven forest cover types *(3)* and is a major component of an eighth, Blue Oak–Digger Pine (Society of American Foresters Type 250), where together with blue oak *(Quercus douglasii)* it forms a climax community in a nearly continuous band around California's Central Valley between valley grasslands and montane forest *(21)*.

Associated trees in the cover type Blue Oak–Digger Pine include California buckeye (*Aesculus californica*), California scrub oak (*Quercus dumosa*), California black oak (*Q. kelloggii*), and interior live oak (*Q. wislizeni*) in the Sierra Nevada; and California buckeye, coast live oak (*Q. agrifolia*), California black oak, and valley oak (*Q. lobata*) in the Coast Ranges. Digger pine also grows with western juniper (*Juniperus occidentalis*) in the Pit River drainage of the Modoc Plateau, and Coulter pine (*Pinus coulteri*) in the southern Coast Range. Predominant shrubs include several manzanita (*Arctostaphylos*) species, primarily *A. manzanita* and *A. viscida*, buckbrush (*Ceanothus cuneatus*), redbud (*Cercis occidentalis*), birchleaf mountain-mahogany (*Cercocarpus betuloides*), silktassel (*Garrya fremontii*), toyon (*Heteromeles arbutifolia*), hollyleaf buckthorn (*Rhamnus crocea*), and western poison-oak (*Toxicodendron diversilobum*).

Digger pine also grows on ultramafic and calcareous soils within several forest types, including Redwood (Type 232) west of Healdsburg, and at the low elevational fringe of Douglas-Fir–Tanoak–Madrone (Type 234) and Pacific Ponderosa Pine–Douglas-Fir (Type 244). Within Pacific Ponderosa Pine (Type 245), Digger pine is found on westerly slopes of the southern Cascades and northern Sierra Nevada. The species also grows in low elevational fringes of California Black Oak (Type 246), Knobcone Pine (Type 248), and in portions of Canyon Live Oak (Type 249) and Western Juniper (Type 238) *(3)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Digger pine is monecious, and strobili appear on short stalks in early spring. Male strobili are 3 to 4 cm (1.2 to 1.6 in) long, green or yellow to reddish purple when immature and light brown when mature. Female strobili are initially small and green or red to purple. When mature they are heavy, ovoid to subglobose, light- to chocolate-brown woody cones. The cone is borne close to the branch on reflexed stalks 5 to 6 cm (2 to 2.5 in) long. Pollination occurs in March through April and archegonia are fertilized in the spring of the next year *(16)*. Cones mature by September or October. Although cones have been noted on 2-year-old trees *(30)*, 10 to 25 years usually must pass to attain full seed production *(16)*. Seeds of Digger pine are large at maturity, averaging 19 to 25 mm (0.75 to 1.0 in) long *(30)*, and weighing up to 1 g (0.04 oz) and more when air-dried *(6)*. Embryos average 18 to 35 mg (0.3 to 0.5 gr) *(9)* and are surrounded by thick seedcoats. Cleaned seeds average 1,280 per kilogram (580/lb) and range between 1,170 and 1,430 seeds per kilogram (530 and 650/lb). Among the American pines, only Torrey pine (*Pinus torreyana*) rivals Digger pine in average seed weight *(16)*.

One of Digger pine's most prominent features is its massive cones, among the largest produced by any pine species. Fresh cone weights average 0.3 to 0.7 kg (0.7 to 1.5 lb) and may exceed 1 kg (2.2 lb) *(7)*. Lengths often reach 20 to 30 cm (8 to 12 in), although mature cones can be much smaller. Large elongated cones are frequently found in populations of the north Coast and Klamath Ranges. Smaller ovoid cones are more common in the Sierra Nevada *(7)*. Prominent features of Digger pine cones are the conspicuous spurs that develop at the base of the cone. Formed from the combined umbo and apophysis of the scale, spurs tend to elongate and recurve, giving the cone a spiny appearance that is fairly constant within a tree, but quite variable within and between populations *(7)*. Unlike most other conifers, Digger pine cones do not form an abscission layer of cells where the cone joins the branch. Thus, cones remain attached long after seeds are shed, unless broken from the tree crown by wind or cut from the tree by the western gray squirrel in quest of seed.

Seed Production and Dissemination—Compared with other species, Digger pine is a consistent seed producer, with large crops produced at 2- to 3-year intervals. Cones may open slowly so that dispersal, beginning in October, sometimes extends into winter. Although open, cones may contain moderate numbers of seeds as late as February *(6,16,30)*.

Digger pine seeds are disseminated in four ways. Wind, usually the primary distributor of seeds for most species, has less influence on Digger pine seeds because wings are poorly developed and seeds are heavy. Birds, primarily the acorn woodpecker and scrub jay, disseminate seed. Gravity also aids distribution of seeds. Digger pine cones, because of their shape and weight, may roll considerable distances on steep hillsides once severed from tree crowns. The large seeds of Digger pine also may roll when dropped from high in the crown. Finally, Digger pine cones are relatively buoyant, with specific gravities varying between 0.59 and 0.96 *(7)*. Cones reaching running water may be transported considerable distances. In one instance, cones were found on a streambank within 13 km (8 mi) of the ocean, and 40 km (25 mi) downstream from the nearest known source *(30)*.

Seedling Development—Seeds of Digger pine show both physiological and physical barriers to early germination when field conditions may be unfavorable. Embryos require a moist, near-freezing chilling period of at least 30 days before germination is possible *(9,13)*. Digger pine growing on sites where winter temperatures fluctuate greatly, such as the Modoc Plateau, may have adapted a longer requirement for chilling to prevent germination until spring. Seeds from populations growing on low-elevation sites with milder winters tend to require less chilling, thereby favoring early establishment before soil moisture becomes limiting *(9)*.

Digger pine's thick seedcoat provides a formidable obstacle to water imbibition and gas exchange, and cracking it or reducing its thickness improves speed and completeness of germination if the chilling requirement is satisfied *(9,13)*. A further physical barrier is the nucellar cap, and removing it improves germination more than seedcoat removal alone *(9)*. No chemical inhibitors of germination in Digger pine seed are known.

Germination is epigeal *(16)*. Seedlings are established best on bare mineral soil and under partial (but not deep) shade. Chaparral cover purportedly helps establishment *(29)*. Cotyledons of Digger pine are unusually large, averaging 49 to 72 mm (1.9 to 2.8 in) in length, and seedlings with cotyledons spanning 20 cm (8 in) tip-to-tip have been noted *(6,8)*. Cotyledon size and number in Digger pine (from 10 to 21 per seedling) help provide enough energy through photosynthesis so that, where soil depth permits, first-year seedlings may develop a deep taproot before soil moisture is depleted in late spring or early summer. Controlled studies show that most of the first season's growth is completed and bud differentiation begins within 5 months of germination. First-year foliage consists mainly of cotyledons and primary needles, although secondary needles (in fascicles of three) may be produced on better sites toward the end of the growing season. Although overall growth is depressed on poor sites, shoot-root ratios tend to be lower as well so that transpiration-absorption deficits may be balanced to some degree *(8)*.

Vegetative Reproduction—Digger pine does not reproduce vegetatively in nature. No information is currently available on artificial reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield—Early growth rates of Digger pine are among the highest of any conifer—an amazing fact, considering the droughty sites on which the species grows. Annual height growth of Digger pine in its native range may average as much as 70 cm (28 in) for the first 8 years after germination *(30)* and often exceeds 1 m (3 ft) during specific years. When introduced to Challenge Experimental Forest in northern California, a very productive Sierra Nevada mixed-conifer site at 790 m (2,590 ft) elevation, dominant and codominant Digger pine averaged 10.3 m (33.8 ft) in height and 19.3 cm (7.6 in) in d.b.h. 15 years after planting *(25)*.

Growth can begin with the first fall rains and continue until soils become too dry in the spring or early summer *(18)*. Within the natural range, high annual rates of growth probably reflect a long growing season that begins early, rather than rapid growth on a daily basis. Digger pine's sparse foliage suggests that daily rates of growth probably are low. On more productive timber sites, the growing season may begin later but extend further into the summer, producing growth rates similar to those on the best low-elevation sites within its natural range. In one study, height and diameter growth rates of Digger pine on a high quality site were comparable, but not superior, to those of native ponderosa pine *(25)*.

The stem form of Digger pine seemingly disregards gravity. Even on steep slopes it may grow nearly perpendicular to the ground. Trees usually maintain a straight, conical form into the pole stage, but mature trees generally are twisted and have multiple forks (fig. 4). The poor form of mature trees probably is a genetic trait but may be traced partly to an open-grown nature that exposes the trees to the damaging effects of wind and to the tendency of lateral buds to elongate when the terminal bud remains static *(6)*. Although Digger pine stands may approach stocking densities of 46 m^2 basal area per hectare (200 ft^2/acre) *(25)*, most stands are stocked much more lightly. Mature trees average 12 to 24 m (40 to 80 ft) in height and 30 to 90 cm (12 to 36 in) in d.b.h. The largest Digger pine officially recorded measured 48.8 m (160 ft) tall, 160 cm (63 in) in d.b.h., and had a crown spread averaging 20.7 m (68 ft) at the widest points *(22)*. Size and age potentials are not determined easily from the trees existing today, because miners, wood cutters, and agriculturalists cleared Digger pine from its best sites more than a century ago. The maximum age reached by this species probably exceeds 200 years.

Rooting Habit—Digger pine produces a deep taproot where soil depth permits. However, hardpan soils are common along the margins of California's Great Valley, and this causes trees to have spreading but shallow root systems with weak taproots extending through duripans. Large trees growing on such sites are windthrown easily during the winter if

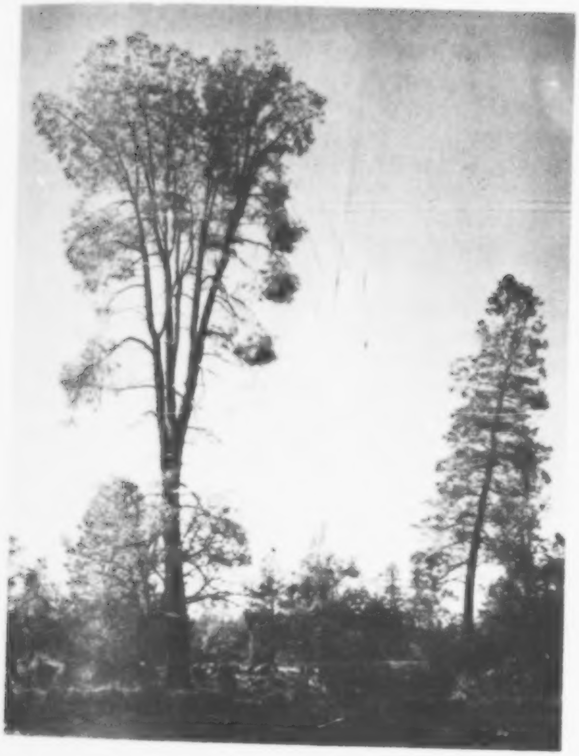

Figure 4—*Digger pine typically has a conical and fairly straight form through the pole stage of development but becomes multibranched with maturity. The larger tree is 25 m (82 ft) tall and 110 years old; the smaller, 17 m (56 ft) tall and 75 years old. The site is a rocky phase of Blue Oak-Digger Pine (SAF Type 250).*

windstorms coincide with waterlogged soil conditions.

Reaction to Competition—Beyond the seedling stage, Digger pine is one of the least shade tolerant of all trees. It is classed as very intolerant of shade. The vigor of Digger pine declines rapidly when competing with such dense-crowned associates as ponderosa pine, blue oak, California black oak, and the live oaks. The wide spacing of Digger pine on xeric sites probably stems from root competition for soil moisture, rather than from mutual competition for light. On mesic sites with better soil development, the sparse crowns of even-aged Digger pine stands allow enough light penetration for needles to persist for 3 years, and stand densities may approach those of moderately-stocked ponderosa pine stands *(25)*.

Digger pine's ability to persist and sometimes dominate on xeric sites on zonal soils probably results from its capacity to photosynthesize throughout the winter and early spring when soil moisture is abundant, and to minimize transpiration losses of water during dry seasons through low foliar biomass and good stomatal action. On zonal soils of more mesic sites, Digger pine cannot compete with forest vegetation. Where they grow together in natural ecotones, ponderosa pine has more stomates per needle than Digger pine and maintains slightly lower leaf water potentials *(33)*. This, coupled with its greater foliar density, gives ponderosa pine a growth advantage where soil moisture is adequate. However, Digger pine's sparse crown (and presumably lower absolute transpiration loss) gives it a sizable survival advantage where soil moisture is scarce.

Digger pine's ability to survive and grow slowly even under severe drought may not be helpful if it is introduced to more mesic sites. During 3 years of normal precipitation at Challenge Experimental Forest, height growth of planted Digger pine averaged 76 cm (30 in) per year—an average almost identical to the 74 cm (29 in) for native ponderosa pine *(25)*. Annual height growth decreased 29 percent in Digger pine during 2 years of drought, however, compared with a decrease of only 12 percent for ponderosa pine.

Digger pine competes well on soils with calcium imbalances. On serpentinite soils, where calcium availability is low and magnesium availability high, Digger pine probably owes its success to low nutrient requirements and preferential absorption of calcium and exclusion of magnesium. These traits have been identified in some populations of ponderosa pine *(14,24)*. On limestone soils, where calcium is abundant, calcium concentrations remain relatively low in Digger pine foliage *(34)*. Results from such extreme soil conditions suggest that Digger pine is unusually effective in regulating its calcium supply.

Damaging Agents—Because of the species' ability to grow throughout the winter, succulent shoots of Digger pine are damaged easily by sudden frosts after periods of mild temperature. Digger pine also is particularly susceptible to damage by wind and hail *(31)*. On sites where winter temperatures fluctuate greatly, stable populations may have evolved such adaptive strategies as delayed germination of seed *(9)*. The thin bark of young trees, along with the species' high resin content and the presence of congealed flows that have dripped from wounds, make Digger pine susceptible to severe damage by fire.

Prominent diseases of Digger pine include western gall rust *(Peridermium harknessii)* and dwarf mistletoe *(Arceuthobium occidentale)*. Western gall rust forms branch galls on Digger pine throughout its range but rarely causes appreciable damage or death. Dwarf mistletoe is a particularly damaging disease that is widely distributed in even the most open stands *(12,26)*. Once infection is established, dwarf mistletoe spreads rapidly *(11)*. Growth loss, deformity, and death often result with the buildup of the disease, and trees of all sizes are susceptible. Digger pine also is susceptible to *Heterobasidion annosum* root disease. This pathogen seldom is a problem in open stands, although the disease can spread rapidly in well stocked stands, such as plantations *(1)*.

Digger pine is host to a wide variety of cone, twig, and foliage insects and is the specific host for *Ips spinifer*, an aggressive bark beetle that often kills trees weakened by fire or drought *(5)*. Heavy production of resin by healthy trees provides a strong defense against many bark beetles, and vapors from its resins are toxic to some *(28)*. Nevertheless, heavy production of resin favors a pitch nodule moth *(Petrova sabiniana)*, which pupates within resin nodules *(5)*. Thick seedcoats provide a protective barrier against damage from most seed insects, but much of the seed production is consumed by rodents and birds. However, predation does not seem to restrict Digger pine's range *(32)*.

Special Uses

Seeds of Digger pine have considerable nutritional value. Their protein and fat contents are similar to those of *Pinus pinea* (a pine of the Mediterranean region whose seeds are harvested for the table), and are equal or superior to those of other commercial species *(4)*. Although Digger pine seeds are not raised commercially, they once were an important supplement to the diet of California valley Indians *(23,30)*.

Digger pine wood has many favorable properties that determine its special uses. Its 0.43 mean specific gravity almost matches that of Douglas-fir *(Pseudotsuga menziesii)*, and its strength properties are comparable with those of ponderosa pine *(27)*. Kraft pulps made from Digger pine rate high in bursting and tensile strength and compare favorably with pulps from most northern conifers *(19)*. Poor form, high resin content, high proportions of compression wood, and low stand density, however, characterize a species commanding only minor commercial interest today.

Currently, the tree's primary value is as a source of railroad tie material, with secondary values for box shook, pallet stock, and chips *(17)*. Digger pine is expensive to log because of its low stand density, and to transport because of its heavy weight and often crooked form. Consequently, stumpage prices are low *(17)*. One of Digger pine's few commercial advantages is that foothill stands can be logged during winter, when species at higher elevations often are inaccessible. Also, some potential exists as stock for shelterbelt plantings on arid sites *(29)*.

Normal heptane, an alkane hydrocarbon of rare occurrence in woody tissues, is the principal constituent of Digger pine wood turpentine and constitutes about 3 percent of needle and twig oil *(20)*.

Genetics

The most obvious variation between Digger pine populations is in cone shape and size *(7)*. Stands in the north Coast Ranges and Klamath Mountains tend to bear large, elongated cones, while those in the Sierra Nevada produce cones that are smaller and ovoid. Variation within a population is great enough, however, that small or large cone races probably do not exist. Early claims of a variety *explicata* *(15)*, based on strongly-hooked cone spurs and relatively long seed wings, are not supported by more recent sampling *(7)*. One isolated Klamath Mountain population, however, tends to have blunt, straight spurs. Cones from the northern part of Digger pine's range tend to have lower specific gravities than those from the southern part.

Seeds collected from sites characterized by cold winters and short growing seasons show the slowest germination rates and require longer chilling periods to achieve full germination *(6,9)*, presumably representing a survival advantage for a species whose seeds normally germinate during winter. Despite the ability of Digger pine to reproduce and grow on extremely infertile soils, such as those formed from serpentinite, no strong evidence has been found that edaphic ecotypes exist within the species *(8)*. Digger pine is resistant to interspecific breeding, and no natural hybrids have been recognized although its range overlaps those of several species of pines. It has been successfully crossed artificially with Coulter and Torrey pines *(2,7,10)*.

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Pinus serotina Michx. Pond Pine

Pinaceae Pine family

David L. Bramlett

Pond pine (*Pinus serotina*), also called marsh pine, bay pine, and pocosin pine, is a medium-sized tree that grows on soils with a high water table. The species name, *serotina*, means "late" and refers to the delayed opening of the cones, up to 2 years before seeds are shed *(11)*. Open cones persist for many years and often become embedded in the growing branches, giving the tree the appearance of being overloaded with cones and a prolific seed producer. One of the largest pond pines grows in North Carolina and measures 94 cm (37 in) in d.b.h., 29 m (94 ft) in height, with a crown spread of 14 m (46 ft) (7). The wood is coarse-grained, resinous, and of fair quality *(2)*.

Habitat

Native Range

Pond pine (figs. 1, 2) grows from Cape May, New Jersey, southward through the Coastal Plains of Delaware, Maryland, Virginia, North Carolina,

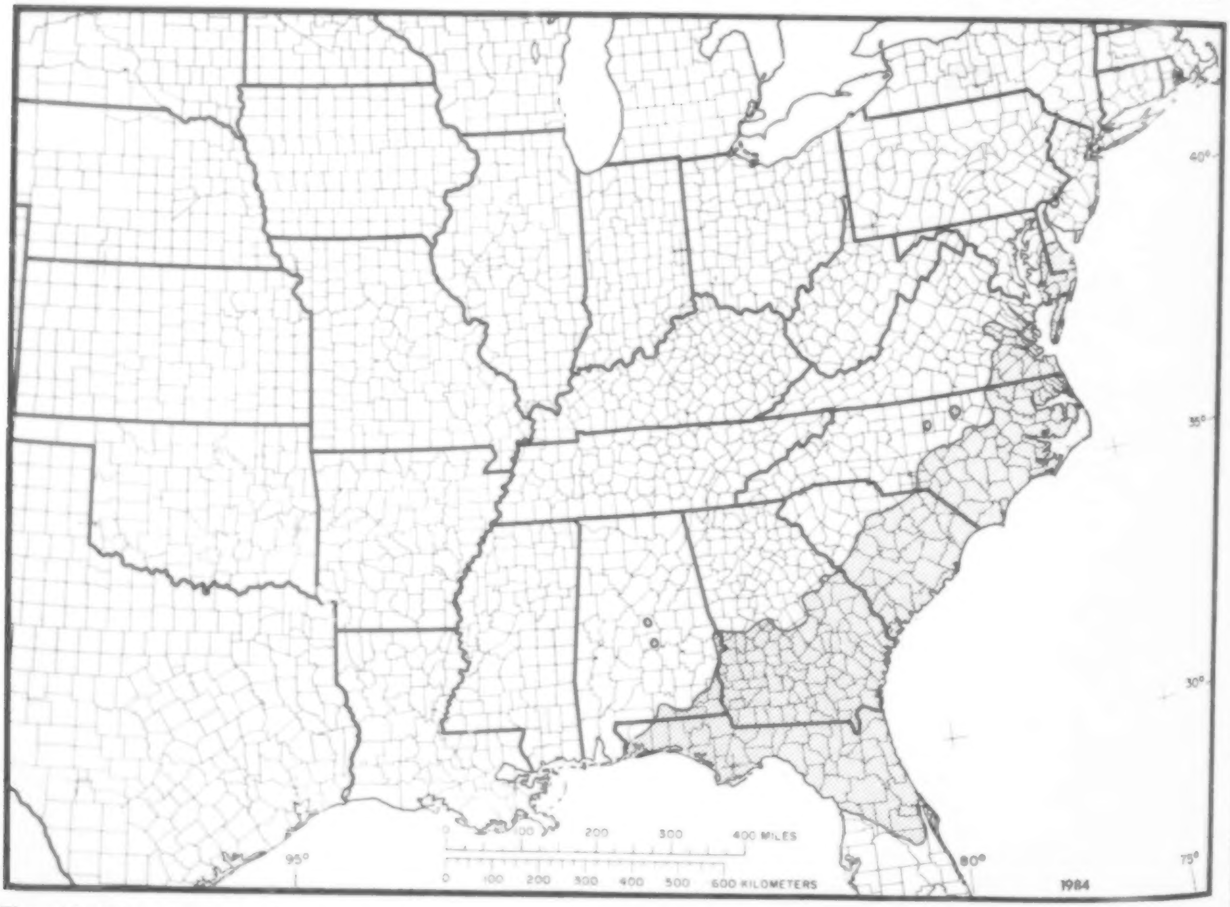

Figure 1—*The native range of pond pine.*

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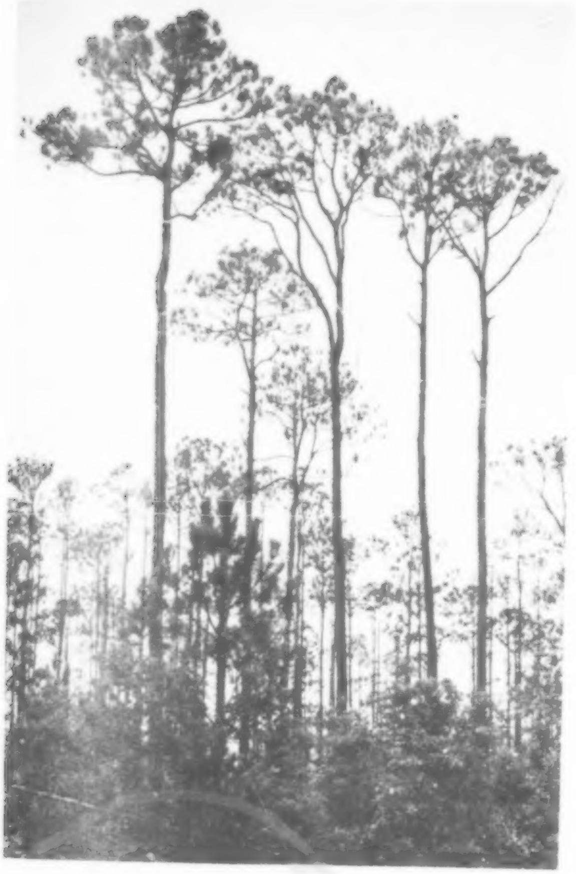

Figure 2—*A group of pond pine (foreground) in Georgia.*

South Carolina, and Georgia to central Florida and southeastern Alabama. Within its native range, pond pine is most frequently found on wet or poorly drained sites.

Climate

The climate throughout the pond pine range is mild and humid. Frost-free days range from 210 in the North to 300 in central Florida. The normal January and February daily average temperature is 2° C (35° F) in the northern range, increasing to 16° C (60° F) for the southern range. In July and August, the normal daily average temperature ranges from 29° C (85° F) in the South to 24° C (75° F) in the North. The extremes of temperature within the range have been as low as -23° C (-10° F) and as high as 43° C (110° F). Annual precipitation increases from 1120 to 1370 mm (44 to 54 in) on a transect from north to south and from 1120 to 1420 mm (44 to 56 in) on an inland to coastal transect. July and August have an average rainfall of 100 to 200 mm (4 to 8 in) per month in contrast to 50 to 100 mm (2 to 4 in) for December and January.

Soils and Topography

The lower terraces of the Coastal Plain in the Southeastern United States are characterized by sandy and organic soils. Typical soils are in the Ultisols order, Aquults suborder, Albaquults and Umbraquults great groups. These soils usually have a dark gray, sandy loam surface soil and a heavy subsoil. The entire area has minor topographic relief and is interspersed with major drainage systems that are frequently very broad. Throughout the region are numerous streams, swamps, pocosins, marshes, and bays that are characterized by poorly developed drainage patterns. The pocosins, in particular, have unique topographic features in the Carolinas. These areas are upland bogs with streams draining from them on all sides. The pocosins have a considerable peat accumulation, frequently as deep as 2 m (6 ft). Also, in the southeastern Coastal Plain there are shallow, poorly drained depressions called bays or ponds. Pond pine is frequently found as the major overstory species in these pocosins and bays in association with a heavy understory of shrubby vegetation.

Although pond pine is most frequently found on poorly drained lands, the species can make excellent growth on mineral soils or on land that is not continuously waterlogged. The slow growth of pond pine is primarily a function of prolonged water saturation and reduced soil aeration. Poor aeration retards decay of organic material and results in the accumulation of muck and peat with high acidity. Although availability of mineral nutrients is usually adequate, nitrogen fixation and nitrification proceed very slowly. Consequently, the amount of available nitrogen is small even though total nitrogen content is high in the undecayed organic matter. Soil saturation also deprives roots of the oxygen required for respiration and growth and tends to keep the soil temperature low *(19)*.

Associated Forest Cover

Pond pine is a major species in the forest cover type Pond Pine (Society of American Foresters Type 98) and is an associate in nine other cover types *(5)*:

81	Loblolly Pine
82	Loblolly Pine–Hardwood
84	Slash Pine
85	Slash Pine–Hardwood
97	Atlantic White-Cedar
100	Pondcypress
102	Baldcypress–Tupelo
103	Water Tupelo–Swamp Tupelo
104	Sweetbay–Swamp Tupelo–Redbay

Other associated tree species are sweetgum *(Liquidambar styraciflua)*, red maple *(Acer rubrum)*, and loblolly-bay *(Gordonia lasianthus)*.

In the pocosins and very wet areas, a great variety of evergreen shrubs form a dense understory. Laurel-leaf greenbrier *(Smilax laurifolia)* is almost always present on pond pine sites. Switchcane *(Arundinaria tecta)* is locally abundant and, as it sprouts prolifically, it is highly favored by periodic burning. Other frequent shrub species include inkberry *(Ilex glabra)*, large gallberry *(I. coriacea)*, zenobia *(Zenobia pulverulenta)*, swamp cyrilla *(Cyrilla racemiflora)*, southern bayberry *(Myrica cerifera)*, sweet pepperbush *(Clethra alnifolia)*, and saw-palmetto *(Serenoa repens)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pond pine is monoecious. Pollen flight and female flower receptivity occur in late March in Florida and about 1 month later in North Carolina. At any given latitude, pond pine flowering is considerably later than that of loblolly *(Pinus taeda)* or slash *(P. elliottii)* pine. It is possible that in some years the flowering period of pond pine may overlap with other southern pines, but hybridization occurs infrequently. Cones ripen in September and October.

Seed Production and Dissemination—Cone production may begin at an early age in pond pine. In eastern North Carolina pocosins, trees less than 10 years old (d.b.h.) produced an average of eight cones per tree. Cone production increased with age and diameter up to 30 years. Seed trees over 30 years (d.b.h.) produced an average of 175 to 200 cones *(19)*.

Mature cones are normally 5 to 10 cm (2 to 4 in) long and remain on the tree for as long as 10 years. Because the cones are serotinous, only a few seeds are released at maturity each year, and the seed crop of several years may be present in an individual cone bearing tree. Viability does not decrease in cones that remain closed for as long as 3 years. Cones open gradually over several years, with two seasonal periods of seed dissemination: April through September and October through January *(4)*.

Like other pine species with serotinous cones, pond pine cones open and release seeds soon after exposure to heat from fire. The intensity of heat does not adversely reduce the viability of seeds; even badly charred cones, following wildfires, release seeds that are capable of germination. In an uncut but burned stand of pond pine, 131,000 seeds per hectare (53,000/acre) were trapped in a 6-week period following the burn.

Mature cones can be opened by exposure to 167° to 169° C (333° to 336° F) dry heat for 30 seconds or by immersion in boiling water for a similar period. An average of 75 to 80 developed seeds are produced per cone and 77 percent of these can usually be extracted. Germination of pond pine seed from North Carolina averaged 44 percent of the extractable seed (including both filled and empty seed) after 60 days *(19)*.

Pond pine seeds are relatively small, ranging from 104,000 to 139,000/kg (47,000 to 63,000/lb) and averaging 119,000/kg (54,000/lb). Seeds are winged and can be dispersed a horizontal distance several times the height of parent trees.

Seedling Development—Adequate moisture is normally available for pond pine germination in the peat and organic soils of the Coastal Plain. Seeds also germinate well on exposed mineral soil. Establishment of seedlings, however, is much better if the competition from weeds, grass, and woody vegetation is reduced by mechanical site preparation or by the use of fire. Germination is epigeal.

Without question, fire has been a major influence on the perpetuation of pond pine in coastal regions of the Southeastern United States. The majority of present-day stands date to a previous wildfire. For natural regeneration, prescribed fires reduce the dense understory of shrubs, prepare a seedbed, and open the serotinous cones. Research in eastern North Carolina indicated that seedling establishment was most favorable in plots that were burned before clearcutting. Clearcutting before burning was also favorable for establishment of an adequate number of free-to-grow seedlings *(4)*. In another study, a headfire was more effective than a flanking fire in the establishment of seedlings.

Techniques for the use of successful prescribed fire for the regeneration of pond pine have been outlined *(18)*. Fires must generally be of high intensity to consume understory shrubs, yet not so intense that serious damage or mortality occurs to the overstory pines. There is usually only a narrow range of weather and fuel conditions where silvicultural objectives and controlled fire can be attained in a given pocosin. Key elements in a prescribed fire plan include light to moderate winds with relative humidities between 35 and 50 percent. The water table also should be close to the surface to prevent spotting and burning of the organic soils.

Seed for regeneration may be provided by seed trees. If seed trees are 23 to 25 cm (9 to 10 in) in d.b.h. and 30 years old, each tree can be expected to produce 5,000 sound seeds. On this basis, 15 to 20 seed trees per hectare (6 to 8/acre) are required to provide adequate seed for establishment. Scarification with fire plows, disks, or logging equipment is sometimes effective in securing seedling establishment but is not as reliable as burning because without heat from a fire seedfall is limited by the serotinous cones of pond pine.

Pond pine seedling growth frequently is limited by excessive soil moisture, low nutrition, and competition from herbaceous and woody vegetation. Under the most severe conditions, seedlings grow only 30 cm (12 in) or less per year. In a pond pine study in a pocosin, seedlings required an average of 18 years to reach a height of 1.5 m (5 ft). The fastest growing seedlings reached this height in less than 10 years *(19)*.

Vegetative Reproduction—Among pine species, pond pine is unique in that it sprouts readily from stumps until quite old. Seedlings or saplings will sprout prolifically when cut, and older trees will sprout vigorously along the stem and branches after intense scorching and defoliation by fire. These sprouts arise from dormant buds in the axils of primary needles of young seedlings. The buds are dormant and are protected by the bark. When the tree is injured, these buds resume growth and may give rise to clusters of buds and numerous short shoots *(19)*.

Not all buds, formed at intermediate and winter-growth flushes, sprout the following spring. Those that do not sprout remain alive; they sometimes develop into short, weak branches and give rise to many lateral buds. They may also put forth secondary dormant buds directly without growing into branches. Buds may also form in needle fascicles, but these are of little importance in the sprouting of pond pine because they are present for only a short time. Thus, pond pine stems and branches bear many clusters of dormant buds that remain alive and capable of sprouting for many years. When trees are defoliated by fire, these buds sprout and give the stems and branches a feathery appearance. Stem sprouting is one of the primary reasons for the low quality of pond pine in frequently burned areas *(19)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Pond pine grows surprisingly well on the better sites with soils that have good internal drainage. In fact, pond pine may be difficult to distinguish from loblolly pine in the sapling stage when in natural or planted stands on comparable upland sites. More typically, however, pond pine is found in the pocosins where it grows very slowly.

Average sizes of pond pine in a North Carolina pocosin were as follows:

Age	Height		D.b.h.	
yr	*m*	*ft*	*cm*	*in*
20	8.5	28	14.7	5.8
50	14.9	49	26.4	10.4
100	20.1	66	35.1	13.8

Stands of pond pine normally have low volumes with seldom over 70 m^3/ha (5,000 fbm/acre). The trees in these stands usually have been repeatedly burned and have poor form and low quality *(19)*.

A well-stocked stand of pond pine at 50 years of age with a site index of 21 m (70 ft) may be expected to have 25.9 m^2/ha (113 ft^2/acre) of basal area and 860 trees per hectare (348/acre), with an average d.b.h. of 19.6 cm (7.7 in). The entire stand might have 179 m^3/ha (2,560 ft^3/acre) of wood inside the bark or 195 m^3/ha (31 cords/acre) of merchantable wood. The total wood volume per hectare could also be allocated as 51.8 m^3 of sawtimber (3,700 fbm/acre) and an additional 146 m^3/ha (23.2 cords/acre) of pulpwood *(16)*.

Pond pine stands with a site index of more than 27 m (90 ft) at age 50 have been measured. These stands could yield 129 m^3/ha (9,200 fbm/acre) of sawtimber and 151 m^3/ha (23.9 cords/acre) of pulpwood. Subsoil texture is directly correlated with site index. Height growth increases with increasing amounts of fine particles (silt and clay) in the subsoil. Other soil properties that are inversely related to site index include depth to mottling, percent of organic matter in the surface soil, and total depth of organic matter *(1)*.

Rooting Habit—No information is currently available.

Reaction to Competition—Pond pine is classed as a species intolerant of shade. It is almost as intolerant as loblolly pine, but less tolerant than slash pine and more tolerant than longleaf pine *(Pinus*

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palustris). Pond pine responds favorably to drainage. In an eastern North Carolina site, basal area and height growth of pond pine were nearly doubled by drainage *(6)*.

On mineral soils, pond pine is an intermediate stage in plant succession. As it is established primarily after fire, it may grow in pure even-aged stands until harvesting or mortality removes the dominant trees. Pond pine stands yield eventually to wetland hardwood species including oaks *(Quercus* spp.), gums *(Nyssa* spp.), hickories *(Carya* spp.), and magnolias *(Magnolia* spp.). In the pocosins, pond pine follows Atlantic white-cedar *(Chamaecyparis thyoides)* when the cedar is killed by fire, but cedar may become reestablished.

Fire maintains pond pine as a subclimax type through sprouting or by stimulating seed dissemination from the serotinous cones. Repeated fires during the dry season, however, may completely eliminate pond pine and produce a grass-sedge bog or savannah. In some large pocosins, woody shrubs, including cyrilla, redbay *(Persea borbonia)*, and gallberry may completely dominate the site for a considerable time.

Almost all stands of pond pine originate from natural regeneration and the species has only infrequently been planted. In a study in the South Carolina Coastal Plain, southern pines were planted on a freshly burned site. The planting site was poorly drained, with a seasonably high water table. After 10 years, slash pine trees averaged 3.6 m (11.8 ft), and pond pine 2.3 m (7.5 ft). This study suggested that the growth of pines on the site was limited by poor nutrition and soil aeration *(8)*.

Damaging Agents—The most serious disease of pond pine is red heart *(Phellinus pini)*, which is common in most of the older pocosin stands. On the Hofmann Forest in eastern North Carolina, 90 to 95 percent of the older pond pines are infected. *P. pini* is a white rot fungus which occurs relatively high in the bole of the tree. It primarily dissolves the lignin of the cell walls, while cellulose is relatively unaffected. Red heart reduces the value of pond pine lumber to such an extent that many stands of sawtimber-size trees may be sold for pulpwood only; and even pulpwood yields are reduced in the severely infected trees *(14)*.

Pond pine is subject to both fusiform rust *(Cronartium quercuum* f. sp. *fusiforme)* and eastern gall rust *(C. quercuum)*, which cause stem and branch cankers on pines and have alternate stages on oaks. In a study of three half-sib families of pond pine, significant differences were observed in rust susceptibility. Pond pine was only half as susceptible to fusiform rust as loblolly pine *(13)*. Comandra blister rust, caused by the fungus *Cronartium comandrae*, has been found on pond pine planted in Tennessee *(3)*. The needle cast fungus *(Hypoderma lethale)* and brown-spot fungus *(Scirrhia acicola)* sometimes cause browning and foliar damage to needles but severe damage is uncommon. *Coleosporium* spp. may attack the foliage but have little effect on tree growth. Pond pine is also attacked by the southern pine beetle *(Dendroctonus frontalis)*, the black turpentine beetle *(D. terebrans)*, and engraver beetles *(Ips* spp.).

In natural stands, numerous pests attack cones and seeds and reduce the final seed crop. Specific insects known to damage pond pine cones and seeds are *Dioryctria* spp. and *Leptoglossus corculus*.

During drought periods, the fire hazard of pond pine sites is extremely high because of the heavy fuel accumulation in the dense understory. Dry fuel weights of the understory and litter layer are frequently more than 22.4 t/ha (10 tons/acre). When fires occur in pocosin areas the excessive fuel and large areas of unbroken forest make fire control extremely difficult. Very intense fires consume not only the trees, shrubs, and litter, but the peat soils as well.

Special Uses

Although pond pine has poor form and slow growth, it produces forest stands of pulpwood and sawtimber where other species will not grow. The pocosins and pond pine stands are considered a major wildlife sanctuary for many wetland species.

Genetics

Population Differences

No definite pattern of variation was found in pond pine wood specific gravity or tracheid length associated with geographic area or depth of organic material in the coastal area of North Carolina *(12)*. Differences in both wood traits were noted among individual plots and among individual trees, however.

The average wood specific gravity of unextracted increment cores of 554 pond pine trees was 0.492 with a standard deviation of 0.049, about the same as the variation among trees in other southern pines. The oleoresin of pond pine is unique for the high proportion of limonene and low proportion of alpha- and beta-pinene.

From a study of 30 traits of pond pine and loblolly pine, slight differences were reported in some Coastal Plain trees compared with those from drier, inland areas *(10)*. Both species, however, had a general uniformity in all locations. Pond pine is included in the North Carolina State Tree Improvement Cooperative. First-generation select trees are located in four seed orchards with a total of 12 ha (29 acres) *(9)*.

Races and Hybrids

Distinct races of pond pine have not been identified. Pond pine hybridizes with several southern pines. Although pitch and pond pine are usually separated geographically, they readily hybridize and intergrade when found together in New Jersey and Maryland. When loblolly pine occurs in association with natural hybrids of pitch and pond pines, hybrids of the complex are frequently found *(17)*. Pond pine also hybridizes with loblolly pine, but in most localities the flowering dates are distinct enough to restrict hybridization. Evidence of introgressive hybridization, however, has been found at several locations in the North Carolina Piedmont and Coastal Plain provinces *(15)*.

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Pinus strobus L. Eastern White Pine

Pinaceae Pine family

G. W. Wendel and H. Clay Smith

Eastern white pine *(Pinus strobus)*, also called northern white pine, is one of the most valuable trees in eastern North America. Before the arrival of white men, virgin stands contained an estimated 3.4 billion m^3 (600 billion fbm) of lumber. By the late 1800's most of those vast stands had been logged. Because it is among the more rapid growing northern forest conifers, it is an excellent tree for reforestation projects, landscaping, and Christmas trees and has the distinction of having been one of the more widely planted American trees.

Habitat

Native Range

Eastern white pine (fig. 1) is found across southern Canada from Newfoundland, Anticosti Island, and Gaspé peninsula of Quebec; west to central and western Ontario and extreme southeastern Manitoba; south to southeastern Minnesota and northeastern Iowa; east to northern Illinois, Ohio, Pennsylvania, and New Jersey; and south mostly in the Appalachian Mountains to northern Georgia and northwestern South Carolina. It is also found in western Kentucky, western Tennessee, and Delaware. A variety grows in the mountains of southern Mexico and Guatemala.

Climate

The climate over the range of white pine is cool and humid. The distribution of white pine coincides reasonably with that part of eastern North America where the July temperature averages between 18° and 23° C (65° and 74° F).

Annual precipitation ranges from about 510 mm (20 in) in northern Minnesota to about 2030 mm (80 in) in northwestern Georgia. In the area surrounding the Great Lakes, about two-thirds of the precipitation occurs during the warm season, April to September. Elsewhere, half of the precipitation occurs during the warm season. The length of the growing season ranges from 90 to 180 days.

Throughout the range of white pine, precipitation is about 1 to 1.5 times the evaporation from shaded free water surfaces *(71)*. Annual potential evapotranspiration is between 430 and 710 mm (17 and 28 in), of which 56 to 68 percent occurs in the warm season. There is a moisture surplus in all seasons.

Average depth of frost penetration ranges from about 25 cm (10 in) in the southern Appalachians to more than 178 cm (70 in) in parts of central and northern Minnesota. Average annual snowfall ranges from 13 cm (5 in) in northern Georgia to more than 254 cm (100 in) in New England and southern Canada *(51)*.

Soils and Topography

The major soil orders found in the white pine range are Inceptisols, Ultisols, Spodosols, Entisols, and Alfisols *(14,50,66)*. In New England the important subgroups are excessively drained or somewhat excessively drained sandy deposits or stratified sand and gravel deposits. Most of the parent materials are glaciofluvial deposits—subgroups Typic Udorthents, Typic Haplorthods, and Typic Udipsamments; glacial tills—subgroups Lithic Dystrochrepts and Lithic Haplorthods; or weathered igneous rocks (loose crystalline fragments mainly from weathered Conway granite)—subgroup Lithic Haplorthods *(42)*.

In northern Minnesota, Eutroboralfs, Haplorthods, Udipsamments, and Hapludalfs are among the most common of the great groups *(2)*. They are similar to the soils of New England and are more or less freely drained and have developed on glacial outwash or till material.

Dystrochrepts, Fragiodults, and Normudults are the major great groups occupied by white pine in the central Appalachian Mountains *(45)*. These soils are weathered from acid shales and sandstones, either in place (residual soils), deposited on lower slopes (colluvial material), or along stream terraces (alluvial material). The soils are generally well drained and have a coarse loamy to a fine loamy texture.

Soils within the range of white pine are derived from granites, gneisses, schists, and sandstones, and less commonly from phyllites, slates, shales, and limestones. In the northern part of the Lake States and southern Canada, white pine is usually confined to soils derived from basalts, gabbro, diabase, and granites *(70)*. Most of the area was covered by the Wisconsin glaciation so the soils are young and have weakly developed profiles *(67)*. In New Hampshire, white pine is found on granite-derived soils and on metamorphic crystalline schists *(42)*. From central Pennsylvania south and in southwestern Wisconsin,

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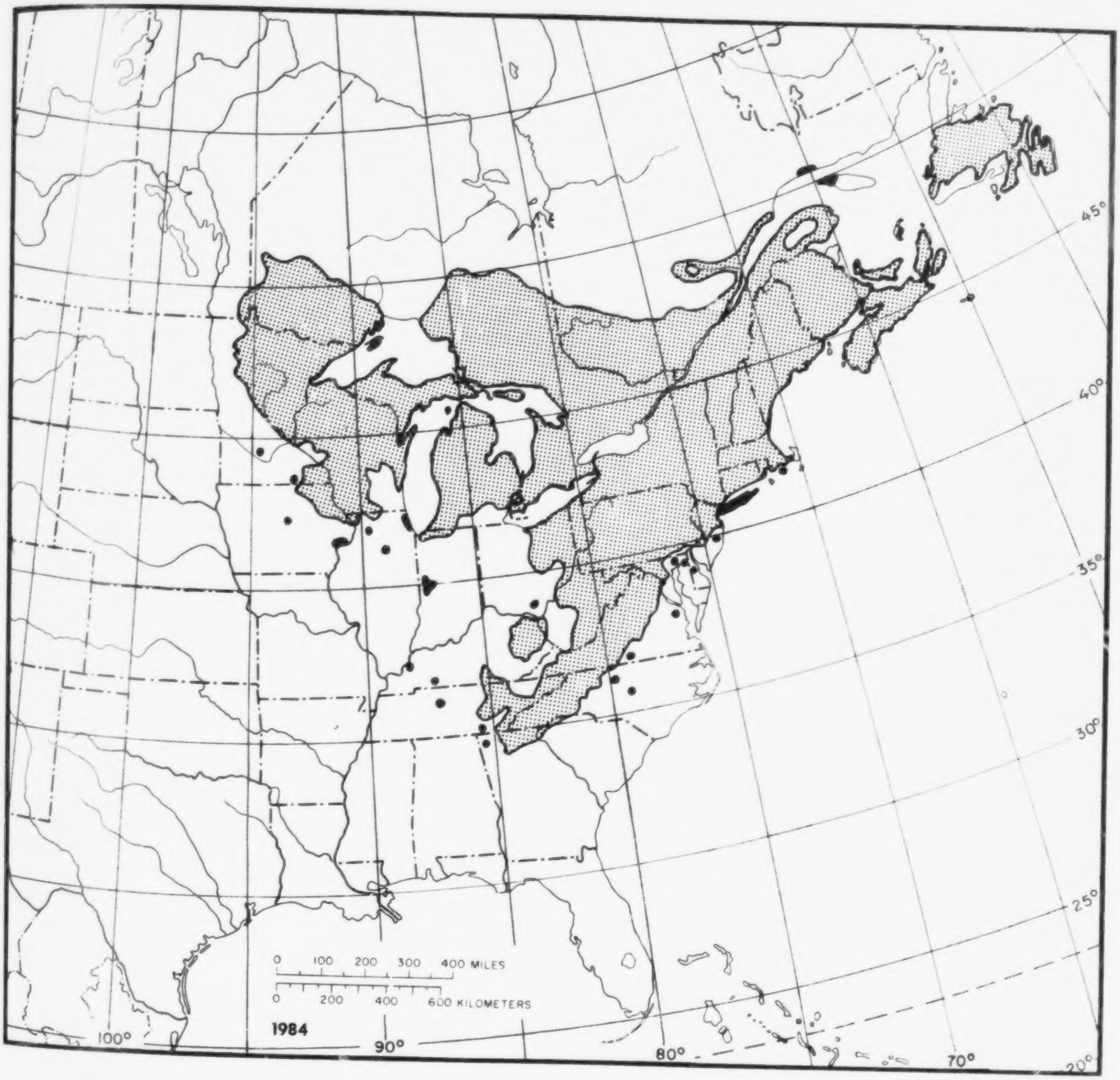

Figure 1—*The native range of eastern white pine.*

the soils are much older, generally are finer textured, and have well developed profiles.

White pine grows on nearly all the soils within its range *(71)*, but generally competes best on well drained sandy soils of low to medium site quality. These soils permit fair growth of white pine but not hardwoods. On these sandy sites, white pine regenerates naturally, competes easily, and can be managed most effectively and economically *(40,47)*. On medium-textured soils (sandy loams), it will outproduce most other native commercial species in both volume and value *(47)*. White pine also grows on fine sandy loams and silt-loam soils with either good or impeded drainage when there is no hardwood competition during the establishment period—as on old fields and pastures, burns, and blowdowns. It has been found on clay soils and on poorly drained or very poorly drained soils with surface mounds. It can be very productive on these sites but usually occurs only as individual trees or in small groups *(47)*. This pine should not be planted in heavy clay soils. Poorly drained bottom land sites and upland depressions are also poor choices for planting *(6)*.

At various places within white pine's range, site quality has been related to combinations of soil and topographic characteristics such as texture and thickness of the A and B horizons, depth and permeability of the underlying rock or pan, depth to the water table, natural drainage class, topographic position, slope percent, and aspect. In the unglaciated regions of Ohio and central Indiana, site quality for white pine increases as the soil becomes coarser in texture and declines as the moisture equivalent and wilting percentage increase in the A and B horizons *(71)*. But thickness of the A horizon had the greatest influence on rate of growth.

In Massachusetts white pine site quality increased with the increase in silt and clay fraction of the A horizon, with higher pH value of the B or C horizon, with increased stone and gravel fraction greater than 2 mm (0.08 in) in the A horizon, with greater nitrogen content in the A horizon, and with higher percent organic matter in the B horizon *(46)*. In general, the higher site indices are associated with the poor soil drainage classes. On reclaimed soils, white pine should not be planted on sites with a pH of less than 4.0 *(6)*.

In New Hampshire, the average height of dominant and codominant trees increased as the soil tended to be less well drained *(7,71)*. Site productivity in Maine showed the following responses: increase with a reduction in soil drainage; increase with pH increases in surface mineral horizons; decrease with increased content of stones larger than 0.6 cm (0.25 in) in the C horizon, but increase with the contents of stones in surface horizon; increase with thickness of the A horizon; increase with soil depth to a bulk density of 1.40 or greater; increase with increasing availability of soil moisture in the upper 76 cm (30 in) of soil *(59)*.

In the southern part of its range, white pine grows best on soils along rivers and streams and grows somewhat more slowly on well drained sites *(22)*. The growth of white pine in plantations in eastern Tennessee was found to decrease with increased plasticity of the B horizon *(71)*.

Pine often grows better than some of its associates on poor soils or sites, such as in northeastern Iowa where white pine was 8 site index points better than oaks on the poor soils *(71)*. In a comparison of site index and growth of 10 species in the southern Appalachians, white pine exceeded all species in growth, except on the best sites, where yellow-poplar outranked it in height only. In New England, white pine frequently pioneers on abandoned agricultural land but only on the well-drained to excessively drained deposits—outwash, sandy tills, and shallow bedrock. White pine may form part of the climax (edaphic) on the driest of these materials or may alternate with oak *(42)*.

In New England and New York, white pine generally grows at elevations between sea level and 460 m (1,500 ft), occasionally higher. In Pennsylvania, the elevation ranges from 150 to 610 m (500 to 2,000 ft) *(71)*. In the southern Appalachians, white pine grows in a band along the mountains between 370 and 1070 m (1,200 and 3,500 ft) above sea level, occasionally reaching 1220 m (4,000 ft). In Pennsylvania and the southern Appalachians, most white pine is found on northerly aspects, in coves, and on stream bottoms. Elsewhere, aspect seldom restricts its occurrence *(71)*.

Associated Forest Cover

White pine is a major component of five Society of American Foresters forest cover types *(70)*: Red Pine (Type 15), White Pine–Northern Red Oak–Red Maple (Type 20), Eastern White Pine (Type 21), White Pine–Hemlock (Type 22), White Pine–Chestnut Oak (Type 51). None of these are climax types, although the White Pine–Hemlock type may just precede the climax hemlock types, and Type 20 is very close to a climax or an alternating type of climax on the sandy outwash plains of New England *(42)*. White pine occurs in 23 other forest types:

1	Jack Pine
5	Balsam Fir
14	Northern Pin Oak
18	Paper Birch
19	Gray Birch–Red Maple
23	Eastern Hemlock
24	Hemlock–Yellow Birch
25	Sugar Maple–Beech–Yellow Birch
26	Sugar Maple–Basswood
30	Red Spruce–Yellow Birch
31	Red Spruce–Sugar Maple–Beech
32	Red Spruce
33	Red Spruce–Balsam Fir
35	Paper Birch–Red Spruce–Balsam Fir
37	Northern White-Cedar
39	Black Ash–American Elm–Red Maple
44	Chestnut Oak
45	Pitch Pine
53	White Oak

57 Yellow-Poplar
59 Yellow-Poplar–White Oak–Northern Red Oak
60 Beech–Sugar Maple
108 Red Maple

White pine also grows with pitch pine *(Pinus rigida)*, jack pine *(P. banksiana)*, shortleaf pine *(P. echinata)*, sweet birch *(Betula lenta)*, bigtooth aspen *(Populus grandidentata)*, quaking aspen *(P. tremuloides)*, black cherry *(Prunus serotina)*, black oak *(Quercus velutina)*, white oak *(Q. alba)*, and various hickories *(Carya* spp.). The ground vegetation in a white pine stand varies greatly, as evidenced by the number of forest cover types in which it is a major or minor component. Beneath pure or nearly pure stands of white pine, understory plants usually are sparse compared to those in the pine-hardwood mixtures *(70)*.

In general, on dry sites the understory vegetation is usually of one or more species of blueberries *(Vaccinium* spp.), teaberry *(Gaultheria procumbens)*, dwarf bush-honeysuckle *(Diervilla lonicera)*, sweetfern *(Comptonia peregrina)*, bracken *(Pteridium aquilinum)*, clubmoss *(Lycopodium* spp.), and broomsedge *(Andropogon virginicus)*. The moist, rich sites support a ground vegetation made up principally of several species of woodsorrel *(Oxalis)*, partridgeberry *(Mitchella repens)*, wild sarsaparilla *(Aralia nudicaulis)*, jack-in-the-pulpit *(Arisaema* spp.), and hay-scented fern *(Dennstaedtia punctilobula)*. Intermediate sites have ground vegetation containing various amounts of the above with dogwood *(Cornus* spp.) and false lily-of-the-valley *(Maianthemum canadense)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—White pine is monoecious. The male strobili are oval, 8 to 10 mm (0.3 to 0.4 in) long and occur mostly on the basal part of new shoots and mostly on older lateral branches in the lower crown. At the time of pollen shed, they are light brown to brown. Female flowers are found most often in the upper crown, primarily at the apical end of the main branches in the position of subterminal or lateral buds *(39)*. At the time of pollination, they are green, and 5 to 38 mm (0.2 to 1.5 in) long. In the northeastern United States, flowering occurs between May and June. The male flowers develop from one to several weeks before the female flowers.

Trees may start to bear female flowers when 5 to 10 years old *(71)*. In the Philadelphia area, quantity production of female flowers does not begin until the trees are about 6 m (20 ft) tall. At that size, 200 to 300 flowers may be produced in 1 year; the number is only a little greater on larger or older trees. Few or no male flowers appear during the early flowering years. Femaleness persists even on older trees 30 to 61 cm (12 to 24 in) in diameter, although trees of this size do produce small to moderate amounts of pollen *(71)*.

The pattern of flowering in white pine is uncertain. In the Philadelphia area, the better flowering trees tend to produce about the same number of female flowers every year, with some exceptions; male flowers, however, do not appear every year *(71)*. Fertilization occurs about 13 months after pollination, and cones mature usually during August and September of the second year *(39)*. Trees have borne cones at 5 to 10 years of age, but good seed production cannot be expected until the trees are 20 to 30 years old *(30)*.

Seed Production and Dissemination—Good seed years are thought to occur every 3 to 5 years, a few seeds being produced in most intervening years. However, at the Massabesic Experimental Forest in southwestern Maine, and at other New England locations, there was virtually no seed produced for 7 years and no good seed crop for 10 years. The major cause of these failures probably is the white pine cone beetle *(Conophthorus coniperda)*.

Cones are green when immature and turn yellow-green to light brown when ripe. Cones that float in linseed oil are considered ripe. Cones should be collected from trees having superior growth and form. Widely spaced dominant trees with full crowns produce the most seeds per cone *(39)*.

In a comprehensive German study of white pine seed production, it was found that a 90-year-old stand produced about 73 kg of seeds per hectare (65 lb/acre); a comparable 60-year-old stand produced only one-fifth as much. In these stands, dominant trees produced twice as many cones as codominant trees *(71)*. In Maine, intermediate density stands 27.6 m^2/ha (120 ft^2/acre) produced 4,430,000 viable seeds per hectare (1,793,220/acre) in a good seed year *(29)*. In high density stands 42.9 m^2/ha (187 ft^2/acre), seedfall was 36 percent less and in low density stands 18.4 m^2/ha (80 ft^2/acre), seedfall was 30 percent less than in the intermediate density stands.

There are 58,400 seeds per kilogram (26,500/lb) with a range from 38,600 to 116,800/kg (17,500 to 53,000/lb) *(39)*. In a study of 250 different parents from all parts of the white pine range, the number of good seeds per cone ranged from 0 to 73. The lowest sets were found in stands at the extremes of the range.

Most of the seeds are dispersed within the month following cone maturity. The seeds travel at least 60 m (200 ft) within a white pine stand and more than 210 m (700 ft) in the open *(71)*. Gray squirrels were found responsible for much of the white pine reproduction under mature red oak stands in southern New Hampshire; they bury and recover the seeds *(3)*.

Seedling Development—Embryo dormancy is common in white pine, and for nursery sowing, stratification of seeds for 60 days at 1° to 5° C (33° to 41° F) is recommended *(39)*.

Germination is epigeal. Bare mineral soil is not necessary for seed germination; seeds can germinate and survive on both disturbed and undisturbed litter layers *(6)*. Under full exposure to sunlight, moist mineral soil, polytrichum moss, or a shortgrass cover of light to medium density are favorable seedbeds. Dry mineral soil, pine litter, lichen, and very thin or very thick grass covers are unfavorable *(71)*.

Unfavorable seedbed conditions can be corrected by scarification or can be overcome by shade. However, dense, low shade such as that cast by slash piles or hardwood brush is adverse to later survival and the shade of young stands of gray birch *(Betula populifolia)* or pitch pine reduces growth in the later stages. Overstory shade resulting from a form of shelterwood cut provides good protection during the early stages of growth and is least damaging to later stages *(71)*.

Experience in North Carolina shows that during years of heavy seedfall white pine seedlings develop well in shade cast by logging debris. Some seedlings may die during a hot dry June, however. Thus, the roughest tracts are reserved and regenerated by natural methods during years of high seedfall only *(52)*. On medium to fair sites in the central Appalachians, white pine seedlings can be underplanted in hardwood stands with reasonable success *(69)*. The hardwoods, mostly oaks and hickories, permit enough light to reach the seedlings so some height growth occurs. Normally 3 to 5 years are required for white pine to become established, and if the pines are released 5 to 10 years later, a high proportion outgrow the competing vegetation. Similar results have been reported for 9- to 20-year-old underplanted white pine in Maine, Canada, and South Carolina *(16,28,71)*.

White pine seedlings in the vicinity of recent pine timber cuttings often are attacked by the pales weevil *(Hylobius pales)*. This insect breeds in the fresh stumps and slash; nearby seedlings are girdled and usually killed. Most of the damage occurs during the first 3 years after a cutting and among seedlings less than 5 years old *(71)*.

After the establishment period, light intensity becomes critical to the survival and growth of white pine seedlings. At light intensities less than 10 to 13 percent of full sunlight, survival is uniformly poor; at least 20 percent of full sunlight seems to be required to keep the seedlings alive. As light intensity increases above this point, growth increases proportionately up to full sunlight unless some other condition becomes limiting *(71)*. Diameter growth of planted white pine increased with increased light in clearcut stands in the Piedmont of South Carolina *(23)*. Height growth of underplanted seedlings after 2 years did not differ from that of seedlings planted in a clearcut.

Although young seedlings can survive for several weeks in soils with moisture below the wilting coefficient, growth at a given light intensity is best in the absence of root competition; growth is better when only an overstory offers root competition than when both an understory and an overstory are competing *(71)*. Mineral soil seedbeds plus light intensities greater than 20 percent full sunlight but less than full sunlight support vigorous seedling growth by reducing surface soil temperatures and providing better soil moisture conditions *(41)*. The survival of white pine 2-2 stock was increased on shallow old pasture soils in eastern Ontario when wedge-shaped pieces of peat saturated with water were placed at the bottom of the planting holes to provide water and prevent desiccation during drought periods *(61)*. Two-0 stock stored in a refrigerator can be planted until mid-June without significant reduction in survival rate. However, seedlings planted in July and August will not be hardened off by the first fall frost *(56)*.

In some early greenhouse and nursery trials with young seedlings, the optimum supply of nitrogen was shown to be 300 p/m; phosphorus, 350 p/m; potassium, 150 p/m; and calcium, 200 p/m *(71)*.

Early white pine growth is slow. Open-grown trees are about 13 cm (5 in) high when 3 years old; 30 cm (12 in) high when 5 years old; and 137 cm (54 in) high when 8 to 10 years old. Thereafter, height growth may be quite rapid. Between 10 and 20 years old, open-grown dominant trees have grown as much as 137 cm (54 in) in height in a single year. Annual increments of 91 cm (36 in) are not uncommon, but average height growth of dominant trees during this period is about 41 cm (16 in) *(71)*. Usually terminal growth occurs within a 30-day period *(6)* and normally is completed by July 1 *(56)*.

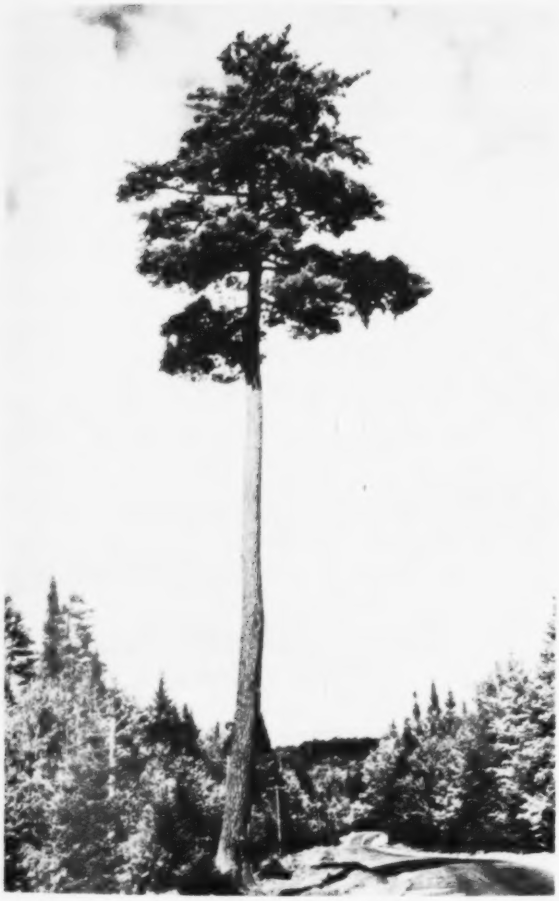

Figure 2—*Eastern white pine, preserved when stand along the Androscoggin River scenic drive in northern New Hampshire was cut.*

Vegetative Reproduction—White pine does not reproduce vegetatively under natural conditions *(31)*. Small cuttings of the last season's twigs, taken in late winter from trees 2 to 6 years old, root fairly readily, however. Within 9 years, outplanted cuttings have developed the same form and size as seedlings, and the root system approaches that of seedlings *(71)*. Also, trees from rooted cuttings performed as well or better than seedling-origin trees when comparing survival, height, and d.b.h. after 40 years *(62)*.

When June-collected cuttings from 17- and 30-year-old white pine were treated with 0.1 percent indolebutyric acid (IBA) and the fungicide Benlate, 60 and 45 percent, respectively, all of the cuttings produced roots in 16 weeks *(36)*. Cuttings from secondary branches of 13-year-old white pines treated with 5 percent benomyl and 25 percent captan fungicides resulted in root formation on 36 percent of the cuttings. When 0.1 percent or 0.5 percent IBA was added, rooting was 31 percent *(64)*. Multiapplications of N^6 benzyladenine at 1,000 p/m to white pine needle fascicles produced roots on 22 percent of all clones tested in 1975 *(17)*.

Scions from the crown of mature trees can be grafted on young stock *(31)*. Side grafts of scions on 3- or 4-year-old white pine stocks seem to be a more reliable method of vegetative propagation than rooted cuttings *(71)*. Buds from main terminal or lateral terminal positions should be used in grafting if early erect growth is desired *(1)*.

Sapling and Pole Stages to Maturity

Growth and Yield—White pine (fig. 2) is a long-lived tree commonly reaching 200 years if undisturbed; maximum age may exceed 450 years. It has a remarkable rate of growth compared to other pine and hardwood species within its range *(20)*. Trees 102 cm (40 in) in d.b.h. and 46 m (150 ft) tall were common in the virgin forests of Pennsylvania, Michigan, and New England *(71)*. In the "National Register of Big Trees" *(54)*, there are two champion white pines: one in Michigan is 168 cm (66 in) in diameter and 48.2 m (158 ft) tall, and the other in Maine is 173 cm (68 in) in diameter and 44.8 m (147 ft) tall.

Periodic height growth increment of dominant and codominant trees in southern Appalachian natural white pine stands occurs at younger ages on the better sites and tends to decline more rapidly. Height growth of both planted and natural white pine is slow during the first 2 to 3 years. Afterwards, growth accelerates rapidly, peaking at an average annual rate of 1 m (3 ft) between 10 and 15 years on site index 80 (base 50 years) *(6)*. By age 55, the rate of annual growth is about equal on all sites *(9)*. For example, in stands with a site index of 36.6 m (120 ft), maximum growth of 1.0 m (3.4 ft) per year occurred at age 14; whereas, with a site index of 18.3 m (60 ft), maximum growth of 0.5 m (1.5 ft) per year did not occur until age 23. By age 55, however, annual growth for all sites was about 0.3 m (1.0 ft) per year (fig. 3).

Diameter growth may be as rapid as 2.5 cm (1 in) per year or as slow as 2.5 cm (1 in) in 40 years. Dominant trees ordinarily grow at the rate of 1 to 2 rings per 5 mm (5 to 10/in) to an age of 250 years. In fully stocked stands on average sites, the average tree diameter increases at a nearly uniform rate of 2.5 cm (1 in) every 5 to 6 years *(71)*.

Generally, rates of growth in basal area, cubic volume, and sawtimber volume in natural southern

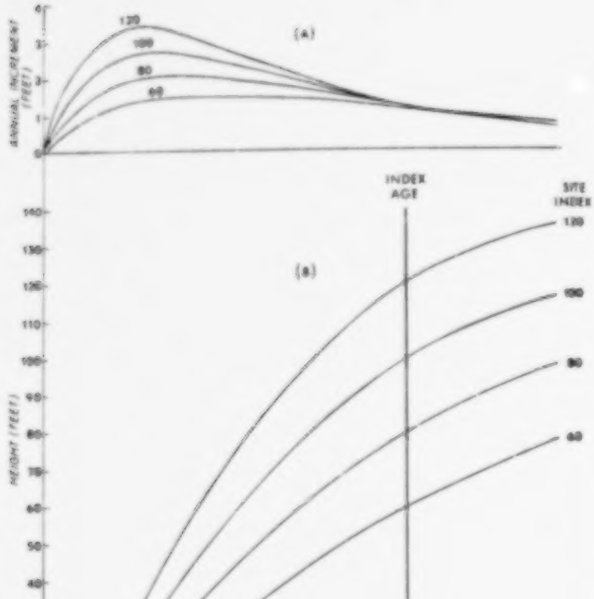

Figure 3—*Curves of annual increment (A) and cumulative height (B) for selected site indices. These curves show the changing pattern of growth with level of site index* (9).

Appalachian stands tend to be slower than those in old-field plantations. For example, maximum mean annual increment in cubic volume occurs at 60 to 70 years in natural stands and at about 25 years in plantations. Similarly, sawtimber volume in natural stands is still increasing at 100 years, though very slowly. In New England stands, mean annual increment in cubic volume occurs at age 40 to 50 *(8)*. Sustained cubic volume growth extends from about age 30 to 90. Mean annual growth peaks at 8.6 m³/ha (615.0 fbm/acre). In New England, a stocking guide for white pine has been prepared *(55)* (fig. 4). The A curve represents 80 percent stocking, and stands above it are considered overstocked. The B curve represents minimum stocking for full site utilization and stands that fall below are considered understocked. Stands between the A and B curves are considered adequately stocked. Where a particular stand might fall in the guide is based on basal area per acre, number of trees per acre, and mean d.b.h. for trees in the main canopy. Tables have been prepared for different stand ages, site and stocking percent, and cubic and sawtimber yield (table 1) *(43)*. Yields of about 504 m³/ha (36,000 fbm/acre) at 50 years in nearly fully stocked managed stands are entirely possible. The average white pine stand in New England grows from 4.2 to 11.2 m³/ha (300 to 800 fbm/acre) per year depending on age, site index, and stocking *(41)*. Site index for eastern white pine is determined from the average height of dominant trees at age 50 years.

For more detailed information, refer to publications on the growth and yield of white pine in natural stands and plantations prepared specifically for the various parts of the range *(6,10,41,49,55,57)*.

Rooting Habit—The form and distribution of the white pine root system vary with the soil characteristics. The normal root system has just a vestige of a taproot. Usually three to five large roots spread outward and downward in the soil, giving the tree a firm anchor under most conditions. In deep, coarse-textured soils, sinker roots that branch from the laterals and grow straight down seem to be fairly common, but they are seldom found in other soils. A concentration of fine roots within the H, A, and B horizons seems to be greatest where the soil is fine textured, with good structure and consistency, and a relatively high moisture equivalent *(71)*. A high total exchange capacity and a relatively high content of exchangeable bases, total nitrogen, and organic matter also favor the concentration of roots.

Much root grafting occurs in white pine stands *(12)*. Regardless of either stand age, soil characteristics, or drainage class, root grafting occurred in 30 to 67 percent of dye-injected trees in five white

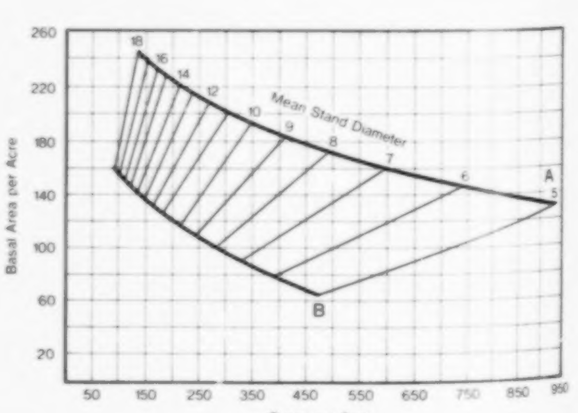

Figure 4—*Stocking guide for nearly pure even-aged white pine stands, showing basal area per acre, number of trees per acre, and mean d.b.h. for trees in the main crown canopy* (55).

Table 1—Yields from fully stocked, natural stands of eastern white pine in New England *(41)*

Stand age (yr)	Site index at base age 50 years 15 m or 50 ft	 21 m or 70 ft	 27 m or 90 ft
		m^3/ha	
Sawtimber[1]			
40	108	209	405
60	236	456	—
80	349	674	—
100	440	852	—
Pulpwood[2]			
20	100	137	187
40	247	339	464
60	334	458	628
80	388	533	731
100	425	583	800
		fbm/acre	
Sawtimber			
40	7,729	14,948	28,909
60	16,858	32,604	—
80	24,898	48,152	—
100	31,460	60,845	—
		ft^3/acre	
Pulpwood			
20	1,423	1,952	2,677
40	3,526	4,836	6,632
60	4,771	6,543	8,974
80	5,550	7,611	10,439
100	6,077	8,334	11,431

[1] Volume to a 15 cm (6.0 in) diameter top outside bark—fbm measured using the International 0.25-in log rule

[2] Volume to an 8 cm (3.0 in) diameter top inside bark

pine stands in New Hampshire, Maine, and Vermont. Exposure of the root systems indicated that often several trees, rather than two or three, were united by root grafts. Root grafting indicates that competition may be a factor in white pine growth for the first 5 to 10 years of a stand. Thereafter, root grafts begin to form, and the stand may function as a union of grafted trees interspersed with individual trees.

Reaction to Competition—White pine is intermediate in shade tolerance, and vegetative competition is a major problem *(60)*. Although it will tolerate up to 80 percent shade, tree growth increases as shade is reduced *(6)*. It can achieve maximum height growth in as little as 45 percent full sunlight *(60)*. In competition with light-foliaged species such as the birches and pitch pine, white pine usually gains dominance in the stand. It can grow successfully in competition with black walnut *(15)*. Against the stronger competition of species such as the aspens, oaks, and maples, however, white pine usually fails to gain a place in the upper canopy and eventually dies *(71)*. Pure stands of white pine seldom stagnate because of inherent variations in vigor. This characteristic is more pronounced on better sites and in natural stands than in plantations *(6)*.

In Ontario, on upland sites white pine and its associates are rated in decreasing order of shade tolerance as follows: balsam fir *(Abies balsamea)*, sugar maple *(Acer saccharum)*, American beech *(Fagus grandifolia)*, eastern hemlock *(Tsuga canadensis)*, white spruce *(Picea glauca)*, yellow birch, white pine, black spruce *(Picea mariana)*, gray birch *(Betula populifolia)*, red oak *(Quercus rubra)*, red maple *(Acer rubrum)*, red pine *(Pinus resinosa)*, jack pine, trembling aspen, bigtooth aspen, and pin cherry *(Prunus pensylvanica) (71)*.

In the seedling stage, white pine is very susceptible to competition because its height growth is slow compared to most of its associates. If white pine survives to the sapling stage, its ability to compete is greatly improved *(71)*.

At either stage, the response to release depends primarily on how strong the competition has been and how long the pine has been in a subordinate position. In general, pines less than 30 years old with at least one-third of their height in live crown respond well, but response declines proportionately with increasing age and decreasing crown length.

White pine may function as a pioneer, as exemplified by its role as the old field pine of New England. It may function as a physiographic climax species on the drier, sandier soils. It may function as a long-lived successional species, and it may be a component of climax forests throughout its range. In Canada, however, it is considered that many of the present white pine stands are edaphic or pyric relicts and that present climatic conditions are against its maintenance as a major species *(71)*.

Pure natural stands of white pine almost never stagnate (fig. 5). Because of differences in vigor, age, and site, differentiation into crown and diameter classes usually occurs. Dominance is more pronounced on the better sites, at the greater stand densities, and in natural stands as compared to plantations *(71)*.

White pine has been regenerated successfully by a wide variety of methods including clearcutting, seed tree, shelterwood, and group selection *(44)*. If there is abundant advanced reproduction, overstory removal is all that is necessary. Clearcutting during or just after heavy seed crops often results in well stocked stands on light soils. Clearcutting in small patches or stands with seed dispersed from adjacent stands is also possible. Because of competition from

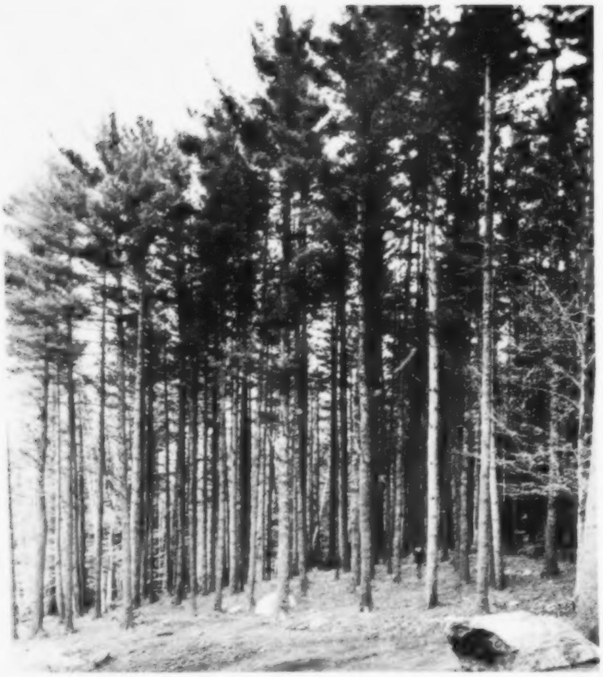

Figure 5—*A stand of pure eastern white pine; such stands are now rare.*

other vegetation and poor seed crops, mechanical site preparation and planting may be necessary sometimes in conjunction with clearcutting.

Where esthetic considerations are important, group selection may have merit. Probably the most versatile reproduction method is the shelterwood method. By control of overstory density with a series of shelterwood cuts, seedbed conditions may be improved; an accumulation of advanced seedlings is obtained over a period of years; protection of seedlings on hot, dry aspects is afforded; weevil attacks are reduced; and competition from herbaceous and hardwood sprout vegetation is suppressed. Two, three, or more cuts spread over a number of years may be used, but usually white pine can be regenerated successfully with a two-cut shelterwood system. Seed cuts should be timed to take advantage of good seed crops, but timing of the final cut is not critical.

Trees in pure second-growth stands of white pine are noted for their limbiness. The limbs live for about 15 years and persist on the trunk for more than 25 years after they die. In the first log of these stands, there is an average of about 60 limbs *(71)*. Pruning has been recommended to increase quality production. If possible, pruning should begin early when branches are less than 5 cm (2 in) in diameter but not before dominance is expressed. At least 25 percent of the live crown and up to 50 percent in closed stands can be pruned without losses in height growth. To realize full benefits of pruning, only potential crop trees should be pruned and stands should be thinned to maximize growth *(24)*. In Canada, pruning is recommended on fast-growing trees in stands 35 to 80 years old because of the inefficiency of pruning smaller trees and the lengthened rotation and probable growth reduction in older stands *(34)*. This recommendation assumes that the highest returns will accrue if the trees are allowed to grow for another 40 years before harvest.

Damaging Agents—There are a total of 277 insects and 110 disease organisms known to attack white pine. Only 16 insects and 7 diseases cause sufficient injury or mortality to be of concern. The three most important are white pine weevil *(Pissodes strobi)*, white pine blister rust *(Cronartium ribicola)*, and *Armillaria mellea (63)*. The white pine weevil kills the terminal shoot, which may include the last 2 or 3 years of growth. The tree is seldom killed unless it is very small; lateral branches from the highest live whorl turn upward to produce new terminal shoots. Bole crook and loss of stem length result from this injury *(71)*. There is evidence that white pine provenances differ in resistance to weevils but even the lowest levels of injury are unacceptable *(25)*.

Among other insect enemies are white pine aphid *(Cinara strobi)*, which causes damage to twigs and branches of large trees and sometimes kills small trees; white pine sawfly *(Neodiprion pinetum)*, which feeds on old and new foliage; Zimmerman pine moth *(Dioryctria zimmermani)*; the Allegheny mound ant *(Formica exsectoides)*, which injects formic acid into the tree tissue; pales weevil *(Hylobius pales)*, which feeds on bark of young twigs and seedlings; pine root collar weevil *(H. radicis)*; European pine shoot moth *(Rhyacionia buoliana)*, which feeds on buds and twigs causing crooked trunks and branches; eastern pine shoot borer *(Eucosma gloriola)*, which attacks terminal needle sheaths, often causing bushiness after repeated attacks; introduced pine sawfly *(Diprion similis)*, which feeds on foliage and may defoliate an entire tree in one season; and white pine cone borer *(Eucosma tocullionana)*, which feeds on white pine cones and is a potentially serious pest *(5)*.

White pine blister rust *(Cronartium ribicola)* is highly virulent throughout the range of white pine. Trees are susceptible from the seedling stage through maturity. Blister rust can cause high losses both in regeneration and in immature timber stands *(71)*.

Red ring rot caused by *Phellinus pini* is the most important heart rot of white pine. The fungus enters through wounds, dead limbs, or tips killed by weevils. Losses are greater in older trees but do not build up rapidly. *Haematostereum sanguinolentum*, a wound parasite, is probably the third most destructive fungus associated with white pine. It usually enters through pruning wounds *(71)*.

Phaeolus schweinitzii causes one of the most common and destructive root rots. A root rot caused by *Heterobasidion annosum* is found particularly on white pines growing on poorly aerated soils. Thinnings appear to increase the incidence of this disease *(71)*. *Armillaria mellea* destroys much of the white pine seedling and sapling reproduction for distances up to 9 m (30 ft) from hardwood stumps. The fungus radiates and girdles pines at the root collar and causes resinosis *(33)*. Other root rots that attack white pine are *Inonotus tomentosus* and *Scytinostroma galactinium*. Many fungi invade white pine foliage. The most serious damage is caused by *Bifusella linearis*, which attacks first-year needles; *Scirrhia acicola*, which can cause spring shedding of all needles; and *Capnodium pini*, which causes surface sooty mold on aphid secretions on needles.

Three categories of nursery diseases are preemergence and postemergence damping off, most commonly caused by *Rhizoctonia solani*, *Fusarium* spp., *Pythium debaryanum*, *P. ultimum*, and *Phytophthora cinnamomi*; damping off and root collar rot caused by the preceding fungi and *Cylindrocladium scoparium* and *Diplodia pinea*; and foliage and succulent stem blights caused by *Cylindrocladium scoparium*, *Diplodia pinea*, *Phacidium infestans*, and *Rhizina undulata*. In the field, seedlings may be attacked by *Armillaria mellea* and by most of the fungi observed in the nursery. In 3- to 10-year-old plantations in Pennsylvania, *Verticicladiella procera* was identified *(65)*.

The bark on exposed roots and the stem in second-growth white pine stands is thin, and fire resistance is low. Losses invariably are heavy after a fire, with mortality continuing for several years. Also, fire injury is probably responsible for introducing disease agents. If fires occurred more frequently than once in 10 years, white pine reproduction might be eliminated *(53)*. Old trees have thicker bark and are at least moderately resistant to fire.

The species is relatively windfirm if permitted full development, but in dense stands, wind damage may be expected from an occasional severe storm, particularly after a recent partial cutting *(71)*. Wind-deformed trees are subject to later compression failures in the bole. Also, white pine is damaged by deer browsing; ice and snow, which often cause limb and stem breakage; sulfur dioxide in stack gases resulting from large scale burning of coal and oil refining; fluorine gas from brick kilns; atmospheric ozone; and sea-salt spray *(11,26,33,58)*.

Special Uses

Although the genus *Pinus* is used by wildlife for food and cover, few specific observations of eastern white pine have been noted. Some species of songbirds that consume seeds of white pine are the yellow-bellied sapsucker, black-capped chickadee, white-breasted nuthatch, pine warbler, pine grosbeak, and the red crossbill. Some mammals that eat seeds, bark, and foliage of white pine are beaver, snowshoe hares, New England cottontails, porcupine, red and gray squirrels, mice, and white-tailed deer *(48)*.

White pines are useful in urban plantings. Trees grown from seeds obtained in Prince Edward Island, Nova Scotia, or in adjacent regions of New Brunswick, Maine, and New Hampshire may be more suitable than trees obtained from other regions *(27)*. They usually have more compact crowns and are more resistant to snowbreak; they grow more slowly, have darker blue-green color, and seem to be more resistant to air pollutants than trees from other origins.

White pine has been used extensively for stabilizing strip-mine spoils. In the anthracite region of Pennsylvania, white pine survived well on spoils that fell within the pH range 5.1 to 6.5, and growth was better on lower slopes of the spoils than on upper slopes *(18)*. On bituminous spoils in West Virginia, white pine survived best on spoils having a pH greater than 4.0 *(13)*. Growth on the spoils was slow for the first 5 years, but total height exceeded that of Scotch pine (*P. sylvestris*), and red pine at 10 years.

The bark of white pine is used as an astringent and an expectorant, and the wood has been used to produce white pine tar, which is used as an antiseptic, expectorant, and protective *(38)*. White pine wood has medium strength, is easily worked, and stains and finishes well. It is used for furniture, patterns, matches, and many other items. White pine is also planted for Christmas trees. The foliage has a good color and responds well to shearing *(19)*.

Genetics

Population Differences

Early provenance tests by the USDA Forest Service and by Genys showed that trees from the southern Appalachians grew more rapidly at a number of test locations. In a followup test, Wright and others collected 177 seedlots from the southern Appalachians. After 12 years, the trees from Georgia and parts of North Carolina and Tennessee grew most rapidly and trees from West Virginia and Maryland grew most slowly wherever they were tested. There are geographic differences in air pollution sensitivity, flower production, winter injury, and susceptibility to blister rust *(4,27,35,73)*. White pine varies greatly in appearance in different parts of its range, suggesting that unidentified ecological or geographical races may exist *(32)*. Likewise, trees immune to white pine blister rust and weevil occur, suggesting the feasibility of selection propagation and breeding of resistant varieties *(72)*.

Races and Hybrids

Eastern white pine is represented in the United States by the typical variety, *Pinus strobus* var. *strobus*. Chiapas white pine, *P. strobus* var. *chiapensis*, is native in the mountains of southern Mexico and Guatemala. Four horticultural varieties have been recognized in Connecticut *(68)*.

Eastern white pine crosses readily with western white pine *(Pinus monticola)*, Balkan pine *(P. peuce)*, blue pine *(P. griffithii)*, and Japanese white pine *(P. parviflora)*. It can also be crossed with limber pine *(P. flexilis)* and Mexican white pine *(P. ayacahuite)* *(21)*. The cross *P. strobus × griffithii* is more vigorous than *P. strobus* in Northern Ohio and more winter hardy than *P. griffithii (37)*.

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Pinus sylvestris L. Scotch Pine

Pinaceae Pine family

Darroll D. Skilling

Scotch pine *(Pinus sylvestris)*, also called Scots pine, is an introduced species in North America, brought here from Europe probably in colonial days. Although it is used for both pulpwood and sawlogs, its principal value in the United States appears to be as a Christmas tree, as an ornamental, and for erosion control.

Habitat

Native Range

Scotch pine has been widely planted in the United States, especially in the Northeast, Lake States, Central States, and Pacific Northwest. It is now considered naturalized in parts of New England and the Lake States *(29)*. The species has also been planted across southern Canada.

Scotch pine is the most widely distributed pine in the world. It grows naturally from Scotland almost to the Pacific Ocean and from above the Arctic Circle in Scandinavia to the Mediterranean. Its altitudinal range is from sea level to about 2440 m (8,000 ft).

Climate

Scotch pine is adapted to a wide variety of climates as indicated by its extremely large natural range. It grows in areas with an annual precipitation exceeding 1780 mm (70 in) and in areas with an annual precipitation as little as 200 mm (8 in). Scotch pine survives in the Verkhoyansk Mountains of eastern Siberia where winter temperatures have been recorded as low as -64° C (-83° F). In some areas it grows where the subsoil is permanently frozen. Scotch pine can also survive high temperatures, and it is found at middle altitudes in the Mediterranean region. The primary distribution of Scotch pine, however, indicates that it is a tree of the continental climates *(18)*.

Soils and Topography

In Europe, Scotch pine grows on a wide variety of soil types. In Scotland it is found on the most ancient rocks and also on the most recent glacial deposits. The cool, humid climate of Scotland, along with the nature of the parent material, which is usually siliceous and acidic, frequently results in a deep litter and raw humus layer. The soils exhibit various degrees of podzolization. Scotch pine grows well on these soils but best growth is on freely drained sands and gravels, often on knolls and terraces. These soils have only a thin layer of raw humus and are weakly podzolized. Although Scotch pine grows on peat land in certain areas, usually it is badly stunted *(18)*.

Studies of the mineral nutrient content of the foliage of several Scotch pine provenances at three sites in Michigan show that Scotch pine has evolved an efficient mechanism to extract nutrients from the infertile sites to which it is relegated in its native range. Significant differences were found among seed sources in their ability to accumulate nitrogen, phosphorus, sodium, magnesium, and boron. Magnesium was one of the key minerals in Scotch pine nutrition at all three sites. The faster-growing seed sources accumulated higher levels of foliar magnesium *(17)*.

Although Scotch pine can grow on soils with pH from 4.0 to 7.0, it grows best on soils in the 4.5 to 6.0 range *(1)*. In the Lake States, Scotch pine is planted most commonly on level or gently rolling sand plains—chiefly at elevations between 300 m (1,000 ft) and 460 m (1,500 ft). In the Eastern States, it has been planted not only on outwash plains, but also on mountain slopes at elevations from a few meters above sea level to about 820 m (2,700 ft) in the Adirondacks. Scotch pine grows well on the loess soils of northern Idaho and eastern Washington, under rainfall conditions prevailing in the ponderosa pine *(Pinus ponderosa)* zone.

Scotch pine grows most commonly on soils in the orders Spodosols, Entisols, Inceptisols, Histosols, Alfisols, and Mollisols.

Associated Forest Cover

Scotch pine has been naturalized in northern New York. The associated trees are black cherry *(Prunus serotina)*, red maple *(Acer rubrum)*, sugar maple *(A. saccharum)*, American beech *(Fagus grandifolia)*, quaking aspen *(Populus tremuloides)*, and eastern white pine *(Pinus strobus)*.

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Life History

Reproduction and Early Growth

Scotch pine, like many of the hard pines, is intolerant of shade. Seedlings germinating under a dense forest canopy do not survive for long. Although the seedlings will grow very well on fertile soil, they are usually found on the more sandy dry soils because of the lack of competition from other trees and plants.

During the last century, Scottish foresters have had serious difficulties establishing Scotch pine regeneration under mature pine stands. This difficulty appears to be partly due to grazing by deer and domestic animals. Successful regeneration has been achieved, however, with the uniform or shelterwood compartment system, which also appears to be successful in the Scandinavian countries *(18).*

The best regeneration is found in stands with the following characteristics: large seed supply, open or light tree canopy, light understory ground cover, and exposed mineral soil or no continuous layer of raw humus *(18).*

In the United States in the Northeastern and Lake States, Scotch pine reproduction is extremely abundant on the more sandy sites. As soon as the parent stand reaches seed bearing age, it begins to spread outward into firebreaks and along open roadsides. In many areas reproduction is so plentiful as to present a mat of seedlings, and this aggressive reproductive habit has concerned foresters who preferred to grow other conifer species on these sites. A recent event in New York may change this reproductive potential of Scotch pine. When scleroderris canker *(Gremmeniella abietina)* is present in the Scotch pine overstory, the advance reproduction can be completely eliminated *(15).* As this disease has advanced across northern New York, the "mats" of Scotch pine reproduction have become seas of dead seedlings. New seedlings continue to germinate under the parent stand but become infected and die within 1 or 2 years. Scleroderris canker is present in Scotland but it is not known whether this disease is related to the reproduction problems there.

Flowering and Fruiting—Although Scotch pine is primarily a monoecious species, some shoots, branches, and even entire trees are predominantly of one sex. Male flower primordia are formed in late summer at the base of the bud that will make the next year's growth. During the winter their presence can be noted as a slight swelling, and the preferred male catkins are easily visible if a bud is dissected. About 2 weeks after growth begins in the spring, the male catkins enlarge to 0.6 to 0.7 cm (0.2 to 0.3 in) long and shed pollen. At this time they are yellow.

The male catkins are borne at the base of the twigs, replacing leaf clusters. They are most common in the lower part of the crown and on short lateral twigs. Because they replace leaves, an excess of pollen production can lead to sparse foliage. A Pennsylvania breeder who selected for early flower production for two generations obtained a variety that produced plentiful pollen but few needles and it was worthless as a Christmas tree.

Female flower primordia are also formed in late summer but are microscopic. They are borne at the tips of buds for the next year's growth. There may be one, two, or three on a single bud. They first become visible after the buds expand in the spring. The primordia enlarge into female flowers or strobili about 2 weeks after growth begins in the spring, at a time when the new growth has completed 75 percent of its elongation for the season. Because of this, shearing of the outside branches such as is practiced by Christmas tree growers removes all female flowers. Indeed, trees sheared in June will not produce seed for the next 3.5 years.

Flowering occurs in late May or early June. On any one tree nearly all pollen is shed and nearly all the female flowers are receptive during the same 2- or 3-day period. In any one stand most trees flower within a day or two of each other. Trees of different provenances may differ in blooming time by several days, however; trees of northern provenances bloom the earliest.

Pollen production tends to be concentrated on short lateral twigs in the lower half of a tree crown. Female flowers are borne on the most vigorous shoots. They tend to be concentrated on upper branches but may occur in any part of the crown receiving full sunlight.

Pollination occurs in early summer, at a time when the female strobili are from 0.6 to 0.7 cm (0.2 to 0.3 in) long. Shortly after pollination, the scales of the female strobili thicken, and the pollen grains germinate and send out a short pollen tube. At this time the female strobili become reflexed instead of pointing forward. For the next 12 months the germinated pollen remains dormant and the female strobili grow little. A little more than a year after pollination, the germinated pollen grains renew growth and fertilize the ovules. In June, soon after fertilization, the conelets rapidly elongate and reach full size by early summer. Seeds mature and cones ripen in early October. The cones require alternating periods of dry and wet weather to open and shed few seed until early winter. Indeed, many seeds are retained on the tree until early spring.

Seeds from any one tree can be sorted visually by color into those that are full and those that are empty—empty seeds are much lighter in color (often nearly white) than full ones. On any one tree the full seeds are fairly uniform in color and size, but both traits vary considerably from tree to tree. Trees from the same stand may produce seeds ranging from tan to almost black and from all one color to speckled. Seed size varies in a geographic pattern—seeds from the extreme northern latitudes are half the size of those from the southern part of the range.

Seed Production and Dissemination—Individual trees in Michigan, under favorable growth conditions, begin to produce male and female flowers at from 5 to 8 years, although the average is between 10 and 15 years *(26)*. Scotch pine continues to produce viable seeds until at least age 200, although seed quality and size are greatly reduced at this age *(18)*.

Good seed crops are produced at intervals of from 3 to 6 years with light crops in most intervening years. The number of cleaned seeds per kilogram ranges from 74,500 to 244,700 (33,800 to 111,000/lb). If properly stored, the seeds remain viable for 15 years. One kilogram (2.2 lb) of average size cones produces approximately 3,300 seeds *(21)*.

Scotch pine cones begin to open in late October, and seed dispersal continues into December. At times, large quantities of seed are dispersed onto snow cover. Seed dispersal for natural restocking of cutover areas is normally limited to between 50 and 100 m (164 to 328 ft) from the parent tree. Maximum seed dispersal is much greater, however. In northern New York, the establishment of second-generation natural Scotch pine seedlings up to at least 1 km (0.6 mi) from the seed source is the rule rather than the exception *(29)*.

Seed crops in New York and Nebraska have been damaged primarily by coneworm larvae *(Dioryctria* spp.). Tip moths *(Rhyacionia* spp.), which destroy shoots bearing newly formed or developing conelets, are common in Scotch pine seed orchards.

Seedling Development—Seeds tested in the laboratory differ in their degree of dormancy according to geographical seed source, individual tree selection, and seed maturity. Most, however, will germinate immediately if placed in warm, moist conditions. Germination is epigeal *(21)*. Artificial light has been shown to increase germination by 83 percent for some seed sources *(4)*.

Field germination is best under full or partial sunlight. Seedling establishment is best when adequate moisture is available and some shade is present. In northern New York, Scotch pine has established itself rapidly on abandoned old fields on very light soils.

At present, almost all the Scotch pine plantations in North America are from planted nursery stock. Two-year-old stock averages from 8 to 20 cm (3 to 8 in) in height. Early nursery practice was to grow the seedlings very close together—from 2,150 to 3,230/m^2 (200 to 300/ft^2) of seedbed. The result was a tall, spindly seedling that bent to the ground when subjected to wet snow during the first winter. These young trees developed a crook at the base. As they developed, the growing tip overcompensated for this crook resulting in an S-shaped stem. The trees eventually returned to a vertical growth habit, but the crook remained. When nursery stock is grown at lower density, 540 seedlings per square meter (50/ft^2), the resulting stock is sturdier and is able to resist snow bending during its early years.

The idea that certain varieties (especially Riga) are always straight wherever grown and that other varieties (such as German and Belgian) are generally crooked is too simple and not always true. Form is as much a matter of site as of variety. On some sites most trees grow crooked whereas on other sites trees of any variety are usually straight. Scotch pine inherently grows straight unless the leader is damaged, when it is apt to be very crooked. The tendency for a variety to be straight or crooked depends on its susceptibility to a particular pest or other damaging agent, and on the presence of that pest or damaging agent in that locality. For example, when the Zimmerman moth *(Dioryctria zimmermani)* is present in high numbers, Greek trees, which are generally not attacked, are straight, while Belgian trees, which are very susceptible, are very crooked. Where pine grosbeaks are present in large numbers, the Belgian trees, which are resistant to this pest, are straight whereas trees of the Riga variety are likely to be crooked.

Poor quality sites seem to have a larger number of pests and a larger number of poorly formed trees than good quality sites.

Scotch pine produces one whorl of branches per year. A fast-growing tree may have branches 0.8 m (2.5 ft) apart resulting in a thin crown. To promote closer branching and denser crowns for Christmas tree production, the trees are sheared by removing the tips of all the new shoots. Following shearing, the leaf fascicles near the cut ends develop adventitious buds. These buds are not formed if shearing is done during late summer.

Scotch pine seedlings grow rapidly in their early years. In Nebraska, after 8 field seasons, trees ranged in height from 2.5 to 5.0 m (8.2 to 16.4 ft) depending on the seed source. Trees from central

European seed grew fastest while those from Scandinavian and Siberian origins grew slowest *(10)*. On good sites throughout the Lake States and the Northeast, trees of the fast-growing varieties can grow 0.8 m (2.5 ft) per year.

In Michigan shoot growth begins in early May in the central part of the State and in mid-May in the Upper Peninsula. The new shoots elongate rapidly and achieve 90 percent of their growth within 3 weeks.

Insects have not been a serious problem under nursery conditions, although a pine shoot moth *(Rhyacionia adana)* has injured some new Scotch pine shoots in several Michigan nurseries *(22)*. The most serious nursery problem of Scotch pine seedlings is *Lophodermium* needlecast, usually attributed to *L. pinastri* but now assigned to *L. seditiosum*. This disease has killed or seriously damaged millions of Scotch pine seedlings in at least 40 tree nurseries in the Northeast, Lake States, Pacific Northwest, and Canada. Nursery stock infected with *Lophodermium* has also been shipped from nurseries to outplanting sites where further damage has occurred in the young plantations *(8)*.

Vegetative Reproduction—In nature, Scotch pine does not reproduce vegetatively. It is not difficult, however, to graft scions from the larger trees onto potted understock of Scotch pine. In a Swedish study, cuttings from young seedlings (50 to 100 days old) rooted readily, but cuttings from shoots of 3-year-old plants rooted poorly *(19)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Scotch pine shows tremendous variation in yield, both by site and by geographic seed source. In seed source tests, some varieties grew 2.5 times as fast as others on the same site *(28)*. The average height of 150-year-old trees in Scotland is from 13.7 to 16.8 m (45 to 55 ft). On well-drained sites, an occasional tree as tall as 22.9 m (75 ft) is found *(18)*.

In a Michigan study in which dominant crop trees were released, the released trees averaged 13.7 m (45 ft) in height and 18 cm (6.9 in) in d.b.h. at 21 years (fig. 1). The plantation was grown from seed from Magdeburg, Germany, and the soil is a fox sandy loam on a well-drained site *(13)*. A 32-year-old, unthinned Scotch pine plantation in the same area averaged 19 cm (7.3 in) in d.b.h. and 18.6 m (61 ft) in height. This seed source was probably central Europe. A Scotch pine plantation in northern New York averaged 26.0 m (85.5 ft) tall and 48 cm (19 in) d.b.h. at age 74 to 77 years. The largest tree in this stand was 29.0 m (95.25 ft) tall and 51 cm (20.2 in) in d.b.h. One of the earliest Scotch pine plantations in the United States was planted in 1879 near Boonville, NY. The seed source was probably southern Germany *(9)*. Although no stand data are available, the largest tree still standing in 1981 was 26.8 m (88 ft) tall and 66 cm (26 in) in d.b.h.

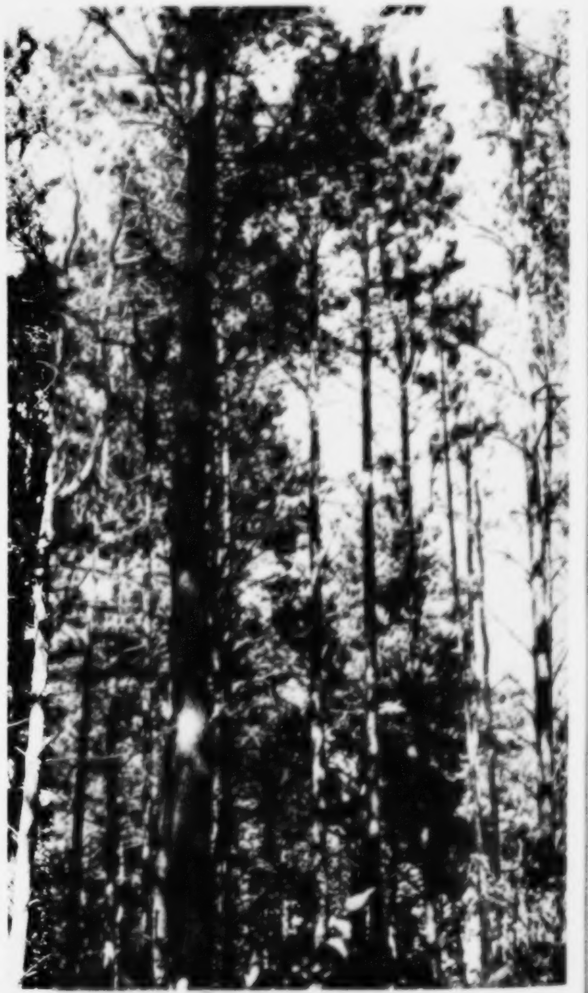

Figure 1—*A stand of Scotch pine grown from seed from a German source.*

Thinning a Scotch pine plantation in southern Michigan increased diameter growth but reduced total volume production *(12)*. At 42 years the unthinned portion of the stand averaged 23 cm (9.2 in) in d.b.h. and contained a volume of 263.8 m³/ha (3,768 ft³/acre). Basal area was 36.0 m²/ha (157 ft²/acre). The area receiving five light thinnings at 5-

year intervals to a basal area of 19.5 to 21.8 m^2/ha (85 to 95 ft^2/acre) had an average d.b.h. of 30 cm (11.8 in) but volume was only 155.2 m^3/ha (2,217 ft^3/acre) and basal area was 25.7 m^2/ha (112 ft^2/acre). The heaviest thinning with five thinnings at 5-year intervals to a basal area of 14.9 to 17.2 m^2/ha (65 to 75 ft^2/acre) produced an average d.b.h. of 34 cm (13.3 in) with 117.5 m^3/ha (1,679 ft^3/acre) of volume and 20.7 m^2/ha (90 ft^2/acre) of basal area.

Rooting Habit—Scotch pine frequently, but not always, develops a taproot. One study in Europe found 64 percent of the trees with taproots. Often, the lateral roots turn and grow down vertically, acting as a taproot. Taproots are more common on sandy soils than on moraine or gravel soils. The average depth of taproots is from 1.5 to 3.0 m (4.9 to 9.8 ft). The bulk of the root system consists of horizontal roots close to the surface. The majority of these horizontal roots are within 20 cm (7.8 in) of the surface. The horizontal root system is smaller on good soils than on poor soils. The depth of the horizontal root system is also related to soil moisture—it is deeper on the drier soils. On vigorous trees, the length of the longest horizontal roots ranged from 4.5 m (14.8 ft) for 14-year-old trees to 17.1 m (56.0 ft) for 52-year-old trees. Root systems on rocky soils are usually shorter than on sandy soils. The size of the stem and the length of horizontal roots are closely interdependent. A small tree will have a small root system regardless of the tree age, and the root system of a large Scotch pine may cover an area of 0.125 ha (0.3 acre) *(5)*.

Reaction to Competition—Scotch pine, like red pine, is intolerant of shade. Overtopped saplings eventually are lost to suppression. Where Scotch pine has been intermixed with red or white pine at planting, the Scotch pine grows so much more aggressively during the first few years that its roots crowd out roots of the other species leaving only Scotch pine.

Many open-grown trees in poorly stocked stands are bushy and crooked with large-diameter branches. This habit appears to be due more to stand stocking than to genetic factors.

Much of the experience with Scotch pine in the United States has been in Christmas tree plantations. In these stands, the trees are usually planted at a spacing of 2 by 2 m (6.6 by 6.6 ft) and are harvested within 8 to 15 years. Early growth in these plantations can be doubled by removing grass and weed competition either by mowing or by using chemical herbicides.

In Norway and Sweden, Scotch pine is normally managed under a uniform or shelterwood system, in compartments of about 4 ha (10 acres). The regeneration cut is made to coincide with a heavy seed year. This can be predicted 1 year in advance because the cones take 2 years to mature. At the time of regeneration, the number of overstory trees is reduced to approximately 50/ha (20/acre) by one or two fellings to provide the required light conditions for young seedlings and to reduce root competition for water and nutrients. The seed trees normally are felled when the reproduction is well established—usually within 5 to 10 years *(18)*.

Damaging Agents—Scotch pine in North America is subject to a number of agents that can severely damage or kill the trees. Some of these agents are not present in Europe and Asia and, as a result, the species has not yet had an opportunity to develop genetic resistance.

Fire and wind can damage the trees. Young stands have thin bark and are heavily damaged by fire. Older trees with thicker bark are moderately resistant. Scotch pine has more branches per whorl than red or white pine and this large number of branches makes the tree weak at the nodes. During severe wind storms, trees may snap off at the nodes 3 to 6 m (10 to 20 ft) above the ground.

Wildlife and insects are also damaging. The pine grosbeak feeds on the terminal and lateral buds of Scotch pine causing numerous small crooks. Trees of Scandinavian provenances are heavily attacked. In Christmas tree plantations, this feeding can cause major economic losses; a single year's feeding can reduce the tree harvest by 50 percent. This is a minor problem to timber growers, however *(2)*. On occasion, porcupine seriously damage Scotch pine plantations by girdling young trees, causing dead tops.

The pine root collar weevil *(Hylobius radicis)* is a major cause of tree death in young plantations in the Lake States. The weevil girdles the tree at the base, killing it within 3 to 4 years. The damage is especially severe on dry sandy soils. The fast-growing central European trees are particularly susceptible *(26)*. In Michigan, on low quality sites, mortality frequently reaches 70 to 80 percent.

The pine root tip weevil *(Hylobius rhizophagus)* causes serious damage in Michigan on Scotch pine Christmas trees grown from stump culture. These trees result from leaving the lower limbs on cut trees to grow into a second tree crop. The pine root tip weevil larvae feed on the roots and root tips, resulting in reduced height growth and flagged shoots, and eventual death. In some cases the pine root tip weevil and the pine root collar weevil attack some

Scotch pine stands simultaneously, causing more mortality than expected from either insect alone *(7)*.

The European pine sawfly *(Neodiprion sertifer)* causes moderate damage in Christmas trees and ornamental plantings. Heavy defoliation reduces growth from 10 to 20 percent. The fast-growing Scotch pine variety *uralensis* shows some resistance to this insect while the slow-growing variety *iberica* is most susceptible *(27)*.

If Scotch pine is pruned in midsummer, the Zimmerman pine moth may be attracted to the fresh pitch. The larvae feed in the cambial region, causing masses of coagulated pitch and frass to collect. Feeding by several larvae at the same whorl may kill the tree top or the entire tree. Partially girdled stems frequently break at the weakened area during storms *(28)*.

The white pine weevil *(Pissodes strobi)* burrows into terminal shoots and kills them. This insect is very damaging to trees on light soils but causes only minor damage on better sites *(28)*. The eastern pine shoot borer *(Eucosma gloriola)* also burrows in the pith of new growth. In Michigan plantations, this insect is universal but causes only minor damage.

The pine spittlebug *(Aphrophora parallela)* is a serious pest in many Scotch pine Christmas tree plantations. Heavy infestations of spittlebugs may cause twig, branch, and tree mortality. In one 19-year-old Scotch pine plantation in southern Michigan, the pine spittlebug has apparently acted as the vector for the fungus disease *Sphaeropsis sapinea*; mortality is now 25 percent and is continuing.

Lophodermium needlecast caused by the fungus *Lophodermium seditiosum* is the most serious disease of Scotch pine Christmas tree plantations. The major loss is due to premature defoliation resulting in unsalable Christmas trees. In general, the longer needle provenances are resistant to this disease. The problem is minor in forest stands *(8)*.

Scotch pine is also a host for brown spot needle disease of southern pines *(Scirrhia acicola)*. This disease, like *Lophodermium*, causes premature defoliation and is primarily limited to Christmas tree plantations. The long needle provenances are also more resistant to this disease *(16)*.

Western gall rust *(Endocronartium harknessii)* is common on Scotch pine in the Lake States and the Northeast. Individual trees may have several hundred galls. In most cases damage is limited to branch mortality and growth loss.

As described earlier, Scotch pine is susceptible to scleroderris canker. This disease is present in many areas in Europe, and as a result, certain Scotch pine provenances show some resistance. Scotch pine is more resistant to scleroderris canker than red pine, and in some areas, red pines have been eliminated from the stand while Scotch pines are still alive. Scleroderris canker can be spread on cut Scotch pine Christmas trees. Therefore, State quarantines have been established to prevent the movement of this disease into noninfected areas *(15)*.

When southern seed sources of Scotch pine are planted too far north of their normal range, severe foliage winter injury develops. This winter injury causes both branch and tree mortality. In the Lake States, a large number of Christmas tree plantations have been destroyed by this problem.

Many of these problems in Scotch pine plantations are the result of planting this species on very poor sites or planting the wrong seed source. Scotch pine has the inherent ability to produce excellent, straight-boled stands under the proper conditions. Hundreds of Scotch pine plantations throughout the Lake States and the Northeast are equal to or better than the best red pine stands. When Scotch pine is planted on very poor sites, however, or when improper seed sources are used, damage by insects is so severe as to make the final stand useless for timber production.

Special Uses

Scotch pine is the most widely planted pine introduced in North America. It is also the preferred large-volume Christmas tree in the United States—approximately 30 percent of the 35 million Christmas trees harvested annually are Scotch pine *(20)*.

Because it survives on poor droughty sites, Scotch pine has been used to control erosion in many areas. However, the poor vigor of many of these stands on dry, infertile sites has made them susceptible to serious insect attack and many of them have little potential to produce timber *(28)*.

Scotch pine has also been used to a large extent in ornamental plantings. It grows better than red pine on compacted clay soils frequently found around homesites. Because Christmas tree plantations are a ready source of trees, many trees are removed from these plantations as ornamental stock. Many Scotch pine have also been planted along roadsides throughout the Lake States.

Scotch pine is similar in fiber and wood characteristics to red pine and is usable for both pulpwood and saw logs.

Genetics

Population Differences and Races

In Europe, seed source studies on Scotch pine go back almost 200 years, and the literature on genetic variation is large. In the United States, an international seed source trial was conducted in 1938. This trial included trees grown from seed collected in Scandinavia and north-central Europe. In 1961, seeds from 162 natural stands and 24 plantations in Europe and Asia were outplanted in 12 test plantations in Michigan. The results of these seed source studies show the extreme importance of beginning with the correct seed source. The fastest-growing varieties from central Europe grew 2.5 times as tall and produced 15 times as much wood as the slowest-growing variety. In Michigan, the variety *carpatica* from eastern Czechoslovakia was most suitable for timber production because of its fast growth and good stem form. The next best was variety *haguenensis* from Belgium, Vosges Mountains of France, and adjacent West Germany. These varieties may perform poorly in other parts of the United States, however. Information on performance of many seed sources is now available for most of the Lake States and the Northeast *(3,6,14,23,27,28)*.

The diversity within Scotch pine is extremely great. A conservative estimate of the number of geographic varieties ranges from 19 to 22. There is also considerable variation within named varieties. Sources differ in many characteristics including seed size, germination, dormancy, and color; cone color; tree form; growth; structure of root system; flowering characteristics; needle color and length; susceptibility to cold, heat, and drought; and resistance to insects and disease. Seed size increases from North to South. In general, southern sources grow faster than northern sources. The more southern sources are more susceptible to low temperatures. The needles of trees from Siberian and Scandinavian seed sources turn yellow in winter while those from Spain, southern France, and the Balkans remain green *(18,21)*.

The only standard names applied to the various geographic varieties are the Latin names published by Ruby and Wright in 1976 *(11)*. Unfortunately, those names are not in common use among seed dealers and nursery managers. Hence, a grower who wants var. *aquitana* from southern France must know that it also goes by the names French Highland, Aquitaine, French Blue, French Green (this name also applies to another variety), and Royal French Blue. Therefore, it is best when ordering nursery stock to specify the region from which the seed should come, that is, Central Mass of southern France, northern Italy, etc. Generally speaking, seed or seedlings ordered in this manner will come true to form. The names Austrian Hill and Riga should be used with particular caution, however, as they may be applied to trees of very different genetic composition.

Hybrids

Hybrids between recognized varieties can be made but are not common. In the Michigan seed source study, one seed source from northern France was evidently a hybrid because it produced trees with characteristics intermediate between varieties *haguenensis* and *aquitana (28)*. Scotch pine can be hybridized with Japanese red pine *(P. densiflora)* and Austrian pine *(P. nigra)*.

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Pinus taeda L. Loblolly Pine

Pinaceae Pine family

James B. Baker and O. Gordon Langdon

Loblolly pine (*Pinus taeda*), also called Arkansas pine, North Carolina pine, and oldfield pine, is the most commercially important forest species in the southern United States, where it is dominant on about 11.7 million ha (29 million acres) and makes up over one-half of the standing pine volume. It is a medium-lived, intolerant to moderately tolerant tree with rapid juvenile growth. The species responds well to silvicultural treatments and can be managed as either even-aged or uneven-aged natural stands, or can be regenerated artificially and managed in plantations.

Habitat

Native Range

The native range of loblolly pine (fig. 1) extends through 14 States from southern New Jersey south to central Florida and west to eastern Texas. It in-

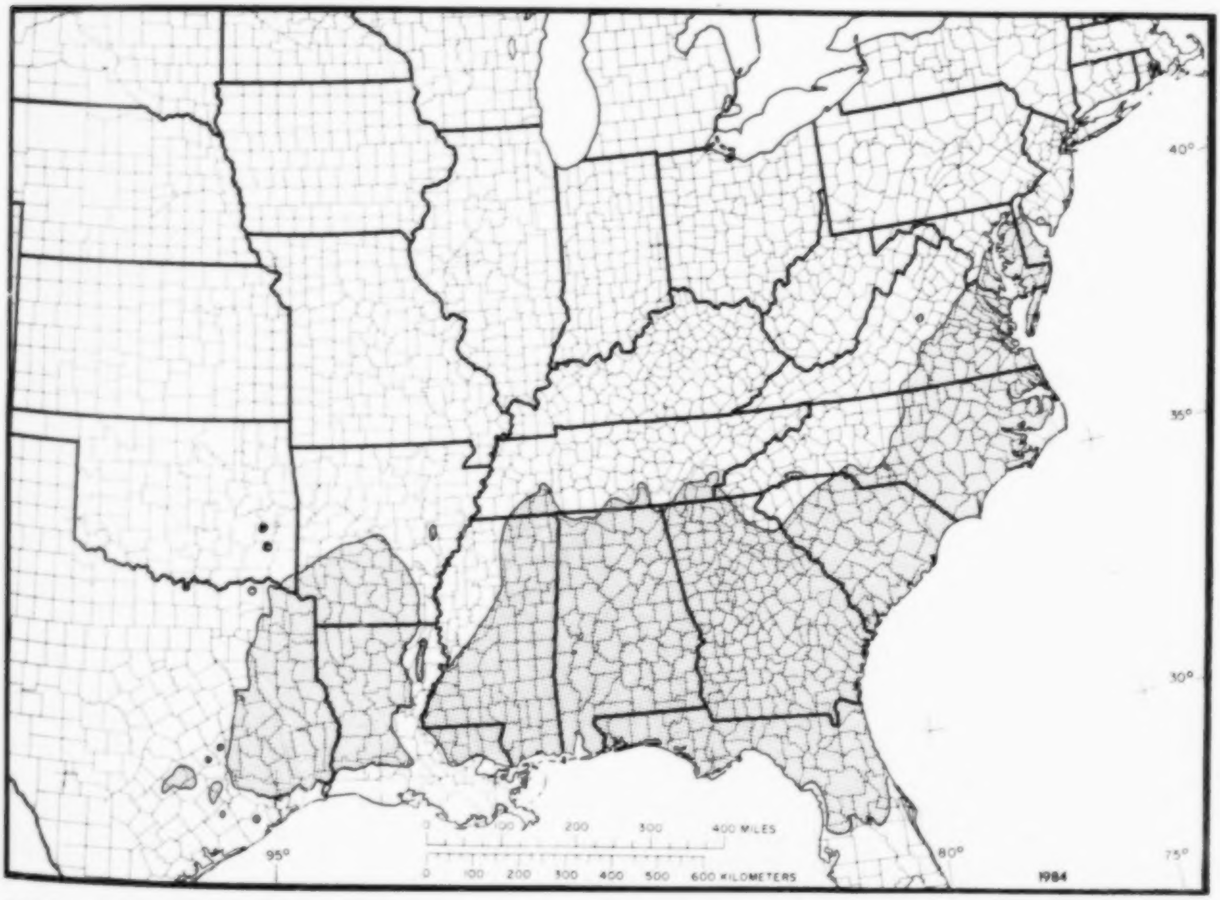

Figure 1—*The native range of loblolly pine.*

The authors are Silviculturist, Southern Forest Experiment Station, New Orleans, LA, and Silviculturist (retired) Southeastern Forest Experiment Station, Asheville, NC.

cludes the Atlantic Plain, the Piedmont Plateau, and the southern extremities of the Cumberland Plateau, the Highland Rim, and the Valley and Ridge Provinces of the Appalachian Highlands. Loblolly pine does not grow naturally in the Mississippi River flood plain and is scarce in the deep, coarse sands of the lower Atlantic Plain and sandhills of North and South Carolina; it is important only in localized areas in southeastern Georgia and northern Florida *(37,55,69)*.

Loblolly pine is an adaptable species that has been successfully planted along the periphery of its natural range and has been introduced on other continents with varying degrees of success.

Climate

The climate over most of the loblolly pine range is humid, warm-temperate with long, hot summers and mild winters. Average annual rainfall varies from 1020 to 1520 mm (40 to 60 in). The frost-free period varies from 5 months in the northern part of the range to 10 months along the southern coastal States. Mean annual temperatures range from 13° to 24° C (55° to 75° F); average July temperature is 27° C (80° F) and frequently exceeds 38° C (100° F). January temperature averages 4° to 16° C (40° to 60° F) and occasionally drops to –23° C (–10° F) in the northern and western parts of the range *(69)*.

During both winter and summer, weather within the range of loblolly pine differs from that immediately outside the range. There are a greater number of days with rain, a greater frequency of effective amounts of rain, that is, more than 13 mm (0.5 in), and higher average winter temperatures. In spring and autumn, the weather within and outside the range is more nearly the same *(37)*.

The main factor limiting northern extension of the species is probably low winter temperature with associated damage from ice, snow, and sleet and cold damage during flowering. Lack of adequate growing-season precipitation probably limits western extension of loblolly pine in Oklahoma and Texas *(37)*.

Soils and Topography

Soils within the native range of loblolly pine are predominantly Ultisols. Small areas of Entisols and Spodosols are found in the Southeastern States and there are some Alfisols throughout the region. Loblolly pine grows on a wide variety of these soils, ranging from the flat, poorly drained Aquults and Aquods of the coastal portion of the Atlantic Plain to the relatively dry Psamments, Udults, and Udalfs of the inland portion of the Atlantic Plain, Piedmont, and upland Provinces *(107)*. Best growth is on moderately acid soils with imperfect to poor surface drainage, a thick medium-textured surface layer, and a fine-textured subsoil. These soils are common in the uplands of the Atlantic Plain and on the flood plains and terraces of rivers and streams. Poorest performance is on shallow soils, eroded soils, and very wet or waterlogged sites *(37)*.

Some typical examples of Ultisols on which loblolly pine grows include the Coxville, Bladen, Beauregard, Wahee, Dunbar, Ruston, Norfolk, Orangeburg, and Smithdale series found in the Atlantic Plain; the Cecil, Davidson, and Appling series in the Piedmont; and the Hartsells and Linker series in the upland Provinces. Ultisols have a site index measured at base age 50 years for loblolly pine of 23 to 30 m (75 to 100 ft) in the Coastal Plain, 20 to 29 m (65 to 95 ft) in the Piedmont, and 18 to 24 m (60 to 80 ft) in the upland Provinces. Typical Entisols on which loblolly pine is found include deep sands (Chipley, Eustis, and Lakeland series) and alluvial soils (Alpin and Osier series), with a site index ranging from 20 to 30 m (65 to 100 ft). Representative Spodosols include the Leon and Lynn Haven series, with a site index of 18 to 26 m (60 to 85 ft). Within the Atlantic Plain but confined to a strip on each side of the Mississippi River are loessial soils represented by the Memphis, Grenada, Providence, Calhoun, and Henry series. These loessial soils, as well as Caddo, Wrightsville, Meggett, and Bude series, all having a site index ranging from 23 to 34 m (75 to 110 ft), are some representative Alfisols on which loblolly pine grows.

In the Atlantic Plain, the productivity of mineral soils generally decreases with improvement in surface drainage. Productivity is sensitive to soil fertility, however, and if fertility is low on poorly drained sites, productivity decreases *(63)*. The presence of a spodic horizon within the rooting zone, as in the Leon series, frequently is associated with low productivity. Deep, excessively drained sands are also very low in site quality unless a water table or a clay lens which holds moisture lies within reach of the tree roots *(37)*.

In the Piedmont Plateau, where surface drainage is well developed, physical characteristics of the soil, rather than surface drainage, determine the availability of moisture, nutrients, and aeration. Here uneroded soils with a thick surface layer and a friable subsoil have a site index of 24 to 27 m (80 to 90 ft). Common series in this category are Appling, Durham, Davidson, Georgeville, and Cecil. The least productive sites are eroded soils with a very plastic subsoil such as the Orange and Iredell series. When the A horizon is gone, site index is less than 12 m (40 ft) *(37)*.

In the Ridge and Valley Provinces loblolly pine site index of 18 to 26 m (60 to 85 ft) generally increases from ridge tops to bottoms. This variation is related to landform, slope position and aspect, and geology. Soil features that determine site quality, such as soil temperatures, surface soil thickness, subsoil consistency, and soil moisture, are correlated with topography. However, past land use, differences in soil parent material, and other factors also affect soil profile development and cause variations in site quality independent of topography *(92)*.

Perhaps as significant as the soils on which loblolly pine grows are those soils in the region where loblolly pine does not grow. These are principally Mollisols of the Blackbelt, Entisols of calcareous river bottoms and terraces (that is, soils in the Louisa, Miller, and Precris series characterized by high base saturation and high pH) and Alfisols of the Coastal Prairie of Louisiana and Texas with moderately high base saturation. These soils may also have other unidentified properties which exclude pine *(72)*.

The topography throughout the loblolly pine range varies from flat near the coast to mountainous in the interior highlands. The topography can best be related to the physiographic regions within the loblolly pine range.

The Atlantic Plain is generally flat near the coast but becomes rolling and hilly inland with elevations ranging up to 150 m (500 ft). The Piedmont Plateau is more rolling, with highly developed drainage patterns and generally finer textured soils. Elevations range up to 305 m (1,000 ft) in Georgia. The Ridge and Valley Province is about 64 km (40 mi) wide and extends into the loblolly pine range from southeastern Tennessee into northern Georgia and Alabama. The topography is characterized by a group of valley floors separated by long, narrow, zigzagging ridges; elevations range from about 185 m (600 ft) to about 365 m (1,200 ft). The Cumberland Plateau, which lies just west of the Ridge and Valley Province, is underlaid by massive sandstone and its topography is characterized by winding narrow-crested ridges and narrow valleys. In some places the sandstone has given rise to local upland flats and mesa-like forms or knobs. Elevations range from 150 m (500 ft) in the southern part of the region and in the valley floors to 305 m (1,000 ft) at the northern end of the region and on ridge tops. The topography of the Highland Rim that extends into south-central Tennessee and northern Alabama is undulating with depressions and low domes where elevations range from 150 to 245 m (500 to 800 ft).

Associated Forest Cover

Loblolly pine is found in pure stands and in mixtures with other pines or hardwoods, and in association with a great variety of lesser vegetation. When loblolly pine predominates, it forms the forest cover type Lobloliy Pine (Society of American Foresters Type 81) *(31)*. Within their natural ranges, longleaf, shortleaf, and Virginia pine *(Pinus palustris, P. echinata,* and *P. virginiana)*, southern red, white, post, and blackjack oak *(Quercus falcata, Q. alba, Q. stellata,* and *Q. marilandica)*, sassafras *(Sassafras albidum)*, and persimmon *(Diospyros virginiana)* are frequent associates on well-drained sites. Pond pine *(Pinus serotina)*, spruce pine *(P. glabra)*, blackgum *(Nyssa sylvatica)*, red maple *(Acer rubrum)*, and water oak *(Quercus nigra)*, willow oak *(Q. phellos)*, and cherrybark oak *(Q. falcata* var. *pagodifolia)* are common associates on moderately to poorly drained sites. In the southern part of its range, loblolly frequently is found with slash pine *(Pinus elliottii)* and laurel oak *(Quercus laurifolia)*.

In east Texas, southern Arkansas, Louisiana, and the lower Piedmont, loblolly and shortleaf pine are often found in mixed stands. In Loblolly Pine–Shortleaf Pine (Type 80), loblolly predominates except on drier sites and at higher elevations. When shortleaf pine predominates, the mixture forms Shortleaf Pine (Type 75).

In fertile, well-drained coves and along stream bottoms, especially in the eastern part of the range, yellow-poplar *(Liriodendron tulipifera)*, American beech *(Fagus grandifolia)*, and white and Carolina ash *(Fraxinus americana* and *F. caroliniana)* are often found in the Loblolly Pine–Shortleaf Pine cover type.

Loblolly pine also grows in mixture with hardwoods throughout its range in Loblolly Pine–Hardwood (Type 82). On moist to wet sites this type often contains such broadleaf evergreens as sweetbay *(Magnolia virginiana)*, southern magnolia *(M. grandiflora)*, and redbay *(Persea borbonia)*, along with swamp tupelo *(Nyssa aquatica)*, red maple, sweetgum, water oak, cherrybark oak, swamp chestnut oak *(Quercus michauxii)*, white ash, American elm *(Ulmus americana)*, and water hickory *(Carya aquatica)*. Occasionally, slash, pond, and spruce pine are present.

In the Piedmont and in the Atlantic Plain of northern Virginia and Maryland, loblolly pine grows with Virginia Pine (Type 79). In northern Mississippi, Alabama, and in Tennessee it is a minor associate in the eastern redcedar-hardwood variant of Eastern Redcedar (Type 46). On moist lower Atlantic Plain sites loblolly pine is found in Longleaf Pine (Type 70), Longleaf Pine–Slash Pine (Type 83), and Slash Pine–Hardwood (Type 85).

In the flood plains and on terraces of major rivers (except the Mississippi River) loblolly pine is a minor associate in Swamp Chestnut Oak–Cherrybark Oak (Type 91). On moist, lower slopes in the Atlantic Plain it is an important component in the Sweetgum–Yellow-Poplar (Type 87). In bays, ponds, swamps, and marshes of the Atlantic Plain it is a common associate in Pond Pine (Type 98), the cabbage palmetto-slash pine variant of Cabbage Palmetto (Type 74), and Sweetbay–Swamp Tupelo–Red Bay (Type 104).

There is a great variety of lesser vegetation found in association with loblolly pine. Some common understory trees and shrubs include flowering dogwood *(Cornus florida)*, American holly *(Ilex opaca)*, inkberry *(I. glabra)*, yaupon *(I. vomitoria)*, hawthorn *(Crataegus* spp.), southern bayberry *(Myrica cerifera)*, pepperbush *(Clethra* spp.), sumac *(Rhus* spp.), and a number of ericaceous shrubs. Some common herbaceous species include bluestems *(Andropogon* spp.), panicums *(Panicum* spp.), sedges *(Carex* spp. and *Cyperus* spp.), and fennels *(Eupatorium* spp.).

Life History

Reproduction and Early Growth

Flowering and Fruiting—Loblolly pine is monoecious; male flowers form in clusters at the tip of the preceding year's growth and female flowers form on the new year's growth. The pollen-bearing staminate flowers are catkinlike in appearance; they range from 2.5 to 3.8 cm (1.0 to 1.5 in) in length and vary from light green to red and yellow depending on stage of development. The pistillate flowers are generally ovoid and range from 1.0 to 1.5 cm (0.4 to 0.6 in) in length. They vary from light green through shades of pink to red depending on stage of development.

Flowering of loblolly pine is initiated in July and August in a quiescent bud that is set from middle June to early July. The male strobili form in this bud in late July and the female in August, but they are not differentiated into recognizable structures until late September or October. In October the staminate buds develop at the base of a vegetative bud and the pistillate buds develop at the apex of a vegetative bud a few weeks later; both remain dormant until early February *(37,41)*. The date of peak pollen shed depends on the accumulation of 353° C (636° F) day-heat units above 13° C (55° F) after February 1 *(16)*. Flowering is also related to latitude, beginning earlier at lower latitudes than at higher ones, and it can occur between February 15 and April 10. Staminate flowers on a given tree tend to mature before the pistillate flowers, which helps to reduce self-pollination. Fertilization of the pistillate strobili takes place in the spring of the following year *(37)*.

Loblolly pine does not normally flower at an early age, although flowering has been induced on young grafts with scion age of only 3 years. The phenomenon of inducing such early flowering in seedlings is dependent on reducing vegetative shoot growth so that quiescent buds are formed in the latter part of the growing season to allow for the initiation and differentiation of reproductive structures. The formation of quiescent buds in seedlings and saplings does not usually occur during that period because four to five growth flushes are common for trees of this age. As a loblolly pine tree ages, the number of growth flushes decreases, which accounts in part for increased flowering of trees at older ages. Flowering is also genetically controlled and is influenced by moisture (May–July rainfall) and nutrient stresses.

Seed Production and Dissemination—Seed production of loblolly pine varies according to physiographic region, climatic factors, and tree or stand condition. In the southern coastal portions of the Atlantic Plain, loblolly is generally a prolific and consistent seed producer, but in some of the inland portions of the Atlantic Plain, the Piedmont, and in the western extremities of its range, seed production is often lower and more erratic. Year-to-year variations in seed crops can range from failure to bumper crops. For example, in 27 years of seedfall records in the Atlantic Plain of South Carolina, there was one seed-crop failure but there were three seed crops of more than 2.5 million sound seeds per hectare (1 million/acre) with the other crops falling between these extremes. At most locations where seed-crop records have been kept, however, such wide annual variations have not been observed.

Despite fluctuations in seed production, loblolly usually produces some seeds every year and good seed crops normally occur at intervals of 3 to 6 years. More than 198,000 sound seeds per hectare (80,000/acre) is considered a good seed crop; 74,000 to 198,000/ha (30,000 to 80,000/acre) is an average crop, and less than 74,000/ha (30,000/acre) is considered marginal, depending on seedbed characteristics and weather conditions.

Throughout the range of loblolly pine, usually cones mature and seeds ripen by the second October after flowering or about 26 months after the strobili are initiated. The mature cones are light reddish brown and range from 7.5 to 15.0 cm (3 to 6 in) in length. They are narrowly conical to ovoid-cylindrical. Each cone scale is tipped with a stout triangular spine. Mature cones have a specific gravity of 0.89 or less (they float in SAE 20 oil). Individual cones may contain from less than 20 to more than 200 seeds, and the percentage of sound seeds may vary from about 15 percent to nearly 100 percent. Loblolly seeds vary in size from 27,100/kg (12,300/lb) to 58,200/kg (26,400/lb) and average 40,100/kg (18,200/lb) *(37,88)*.

Seed production of individual trees increases with tree age, size, and freedom from crown competition. By age 25, enough seeds may be produced in widely spaced trees to regenerate a stand; however, trees at 40 years generally produce three to five times more. Rotations shorter than 30 years usually do not lend themselves to natural regeneration.

In well-stocked and overstocked stands, cone production of loblolly pine can be stimulated threefold to tenfold by releasing the seed trees from competitors at least three growing seasons before the seed is needed. If seed-tree release is delayed later than May 1, seed-crop stimulation will be delayed 1 year. In overstocked stands, if seed trees are not released before a harvest cutting, then seed-crop stimulation will be delayed 2 or 3 years, depending on the season of the harvest cut *(37,61,95)*.

Seedfall usually begins in October, and the bulk of the seeds are released in November and early December. Seedfall is hastened by dry, warm, windy weather and retarded by cool, wet weather. Seed dispersal in or adjacent to a stand varies with height and stocking level of the seed-source trees, magnitude of the seed crop, terrain, and weather conditions at the time of seedfall. The effective seeding distance ranges from 61 to 91 m (200 to 300 ft) in a downwind direction from the seed source and 23 to 30 m (75 to 100 ft) in other directions. Viability of seeds varies with seed-crop size and the month that the seed is dispersed. Seed viability is often lower in years of poor seed crops and in seeds dispersed late in the season *(37)*.

Loblolly pine seeds generally go through a stage of dormancy after seedfall, which lasts longer than that of any other southern pine. Seed dormancy is related to the impermeable properties of the seedcoat that constrain water imbibition and oxygen uptake; chemical germination inhibitors do not play a significant role *(11,73)*. Dormancy is broken naturally as the seeds overwinter on the forest floor. Germination is epigeal *(88)*. Natural seed germination usually begins in March when daytime temperatures range between 18° and 27° C (65° and 80° F). Few seeds remain viable (not more than 0.1 percent) on the forest floor for germination in the second year after seedfall *(70)*. Secondary seed dormancy can be induced during seed handling procedures. Cold, moist stratification of the seed for 30 to 90 days at temperatures 3° to 5° C (37° to 41° F) are generally recommended to artificially break dormancy for direct seeding or for nursery sowing *(74)*.

Seedling Development—Moisture is a critical factor in seed germination and seedling establishment; the amount of rainfall in the spring is related directly to seedling catches. Scarifying the seedbed exposes mineral soil and increases contact of the seeds with moist soil surfaces. Failure of the root radicle to penetrate compacted or puddled soil surfaces reduces seedling establishment, especially on major skid trails and log decks. Soil compaction and puddling also reduce root growth, seedling survival, and shoot growth *(36,37,40,61)*.

Seedbed preparation by scarification or burning greatly increases seed germination and seedling survival, which reduces the number of seeds required to produce one seedling. For example, undisturbed seedbeds with a litter depth of 8 to 10 cm (3 to 4 in) require 5 to 6 times more seeds to produce the number of seedlings produced in disturbed seedbeds.

Seed germination decreases with age of seedbed and increases with clay content of the soil. Two-year-old seedbeds require 3 to 4 times more seed for successful establishment than do 1-year-old seedbeds, and 3-year-old seedbeds require 9 to 14 times more seed than is needed in the first year. Thus, favorable seedbeds usually exist for only 1 year after disturbance, after which they rapidly deteriorate. Heavier textured soils provide better seedbeds which results in higher seedling survival than do lighter textured soils *(37,104)*.

Drought is a major cause of mortality for planted loblolly pine seedlings, especially in areas with low rainfall during the growing season. Improper care, handling, and planting of nursery stock and inadequate site preparation for control of competing vegetation also contribute to poor survival by indirectly increasing moisture strees *(34,57)*.

Height growth of loblolly pine seedlings occurs annually in a series of two to five growth flushes and is dependent on variables such as temperature, day length, soil moisture, nutrients, competition, and genetics. Temperature has a dominant influence on the initiation of height growth in the spring. High day temperatures increase height growth, but high night temperatures decrease it. When day and night temperatures differ by 12° to 13° C (54° to 55° F), the best height growth occurs *(15,43)*.

Soil moisture influences growth of loblolly pine by its effect on internal water relations and vital physiological processes. Growth is reduced with increasing water deficits. For example, at a soil moisture tension of 1520 mm of mercury (2 atm), height growth of loblolly pine seedlings is greatly reduced and at 2660 mm of mercury (3.5 atm), height growth ceases. Height and diameter growth are significantly reduced by a late spring and summer drought, which also reduces early height growth the following year *(37,98,116)*.

Growth of loblolly pine seedlings in a natural stand is inversely related to overstory stocking of pine and hardwoods. As the proportion of hardwoods increases for a given pine stocking, loblolly pine seedling growth decreases. Size and shape of openings affect seedling growth up to 9 m (30 ft) from edges of openings. Seedlings growing beneath overstory hardwoods are not likely to survive more than a few years and if they do survive their growth will be slow. Growth and survival of loblolly pine seedlings during the first 7 years after a stand is regenerated may be reduced by 80 percent because of the faster growth of competing hardwood sprouts and shrubs. Pine seedlings not overtopped by hardwoods at age 3 or older have an excellent chance to outgrow the hardwood competition *(37)*.

Photosynthesis in loblolly pine seedlings is related to light and soil moisture conditions, which in turn are affected by competing hardwoods. Photosynthetic rates of many hardwoods are inherently higher than those of loblolly pine at relatively low light intensities and with low soil moisture *(37)*.

Fertilization often increases seedling growth in waterlogged soils. In some instances where specific nutrients are limiting growth, fertilization results in growth equal to or greater than that with drainage. Loblolly pine grows well on wet, fertile sites because of the effects of moisture on nutrient availability *(63,101)*.

Vegetative Reproduction—Young loblolly pine seedlings up to 3 years of age may sprout from buds in axils of primary needles if tops are clipped off, but older trees will not produce basal sprouts at root collars if stems are cut or top-killed by fire, nor do they produce root sprouts. Rooting is related to tree age and is more successful with cuttings from younger trees. Techniques and materials used to root cuttings are of critical importance. For example, a fine mist over the rooting bench is better than a heavy mist, and Hare's powder is a better compound to use than indolebutyric acid when rooting loblolly pine cuttings. Although needle bundles and buds of loblolly pine have been rooted, the success rate has been low. Air layering, a modification of rooting cuttings, has been the more successful method of the two. Success rates have been high for young trees but older trees are more difficult to air layer *(29,42,48,110)*.

Grafting is the most common method of vegetative propagation used to produce genetically uniform trees, especially in seed orchards. Grafting success is usually high but varies with scion material because problems may develop from incompatibility of scion and root stock *(29,37,66)*.

Producing genetically uniform plantlets from tissue cultures is a promising technique, and research is underway to develop procedures for the commercial production of loblolly pine clones *(19,94)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Growth of loblolly pine stands is inherently good when compared to most hardwood competitors and on many sites doubles or triples the production of common associates *(108)*. Growth is influenced by the physical and chemical properties of soils (texture, compaction, aeration, moisture, pH, nutrients), light, temperature, photoperiod, allelopathy, precipitation and its seasonal pattern, and intra- and inter-species competition for space and essential elements. Because many of these factors interact, it is difficult to specify the most limiting one. Consequently, these biotic and environmental effects are commonly expressed as the average height of dominant trees at age 50 years, that is, site index.

Yield estimates for natural, even-aged loblolly pine (fig. 2) in fully stocked stands were first made more than 50 years ago *(3,106)*. Additional estimates have been made in more recent years for stands of various stocking levels *(18,81,90,99)*.

Normal yields of natural, even-aged loblolly pine stands on average sites, such as those with a site index of 27 m (90 ft), have ranged from 133.0 m^3/ha (1,900 ft^3/acre) in trees 9 cm (3.6 in) and larger in d.b.h. including 29.4 m^3/ha (2,100 fbm/acre) in trees 24 cm (9.6 in) and larger d.b.h. at age 20 to 427.7 m^3/ha (6,110 ft^3 or 40,000 fbm/acre) at age 60 (all board-foot volumes reported in International quarter-inch rule). Mean annual cubic volume growth generally culminates at about age 40 on these sites with approximately 8.0 m^3/ha (115 ft^3/acre). As a result of larger sawtimber merchantability limits, mean annual board-foot growth culminates at about age 50 at a rate of 9.5m^3/ha (680 fbm/acre).

Growth of loblolly pine may be affected adversely by drought, excess moisture (flooding), and nutrient deficiencies. Growth of this species is highly corre-

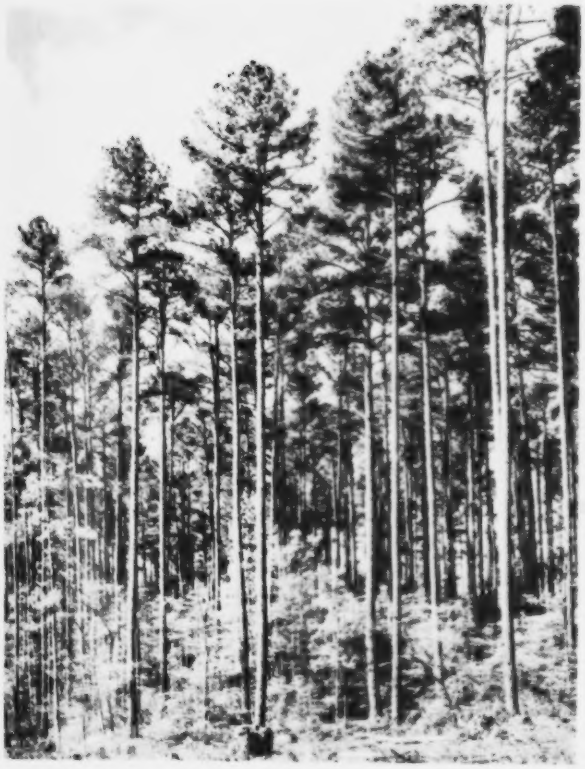

Figure 2—*Old-field stand of natural, even-aged loblolly pine.*

lated with departure from the normal rainfall of April through October. Extreme negative and positive departures (−117 vs. 229 mm or −4.6 vs. 9.0 in) in seasonal rainfall over 21 years resulted in differences of nearly 2.1 m^3 (74 ft^3) of annual growth *(12,39,65)*. Drainage (including bedding) and fertilization have been shown to increase dominant height and basal-area growth, resulting in dramatic increases in volume growth *(45,63,76,101)*.

Growth of planted loblolly pine is affected by the same factors affecting natural stands. Sites are usually prepared before planting on cutover lands, and some are fertilized to correct nutrient deficiencies. Such practices are applied to control competition and to supply nutrients at optimum levels to establish vigorous, uniform stands at spacings that will fully utilize site potentials (fig. 3).

Yields of planted loblolly pine vary with plantation age, site quality, number of trees planted, and interactions of these variables. Yields generally increase with increasing age and site quality. Yields also increase with higher planting density or closer spacing; however, on some sites, moderately wide spacing of 2.4 by 2.4 m (8 by 8 ft) or 3.0 by 3.0 m (10 by 10 ft) outproduce both wider and closer spacing. Mean annual increment culminates at younger ages on better sites than on poorer ones. Better sites can carry more stocking than poor sites; consequently, initial spacing can be closer *(9,77,93)*.

Closer spacing tends to produce higher total cubic volumes at younger ages than does wider spacing; however, average tree sizes are larger on wider spacings than on closer ones. If sawtimber is a primary management objective, then wider spacing or lower density would be advantageous. Although thinning seldom increases cubic volume yield of loblolly pine, light thinnings that salvage suppressed and moribund trees have increased net yields by as much as 20 percent in 50 years. Thinnings usually result in increased diameter growth of residual trees and allow the growth to be put on the better trees in the stand. Another benefit is that thinnings provide intermediate returns on investment *(2,17)*.

Average total solid-wood yields of unthinned loblolly pine planted at 1,730 seedlings per hectare (700/acre) on non-old-field sites at various locations within its range were predicted to increase from ap-

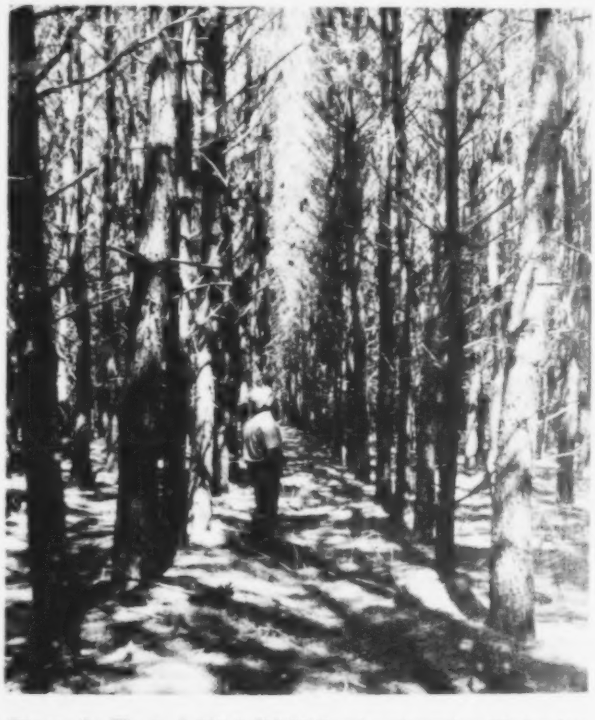

Figure 3—*The A. J. Mitchell loblolly pine plantation, Wadmalaw Island, SC, at age 12.*

proximately 155 m³/ha (2,200 ft³/acre) at age 15 to 300 m³/ha (4,200 ft³/acre) at age 30. Mean annual increment at age 30 was about 10 m³/ha (145 ft³/acre) *(1,4,27,33,67)*. Estimates are also available for a variety of site and stand conditions and geographic areas *(8,21,22,23,25,44,68,71)*.

Growth and yield in natural uneven-aged loblolly pine stands is dependent on stand structure, stocking, and site quality. To optimize average annual growth on average sites with a site index of 27 m (90 ft), stand structure should be manipulated so that approximately 70 percent of the merchantable cubic volume is in the saw-log portion of the stand, that is, trees 25 cm (10 in) in d.b.h. and larger. On average sites, stands with approximately 17 m²/ha (75 ft²/acre) of basal area, or 140 m³/ha (2,000 ft³/acre) total merchantable volume, or 10,000 fbm saw-log volume at the end of the cutting cycle would be considered well stocked *(5,84,86)*.

On good sites in southern Arkansas, with a site index of 27 m (90 ft) managed uneven-aged loblolly pine stands that are well stocked have averaged 0.7 m²/ha (3 ft²/acre) of basal-area growth, 5.6 m³/ha (80 ft³/acre) of merchantable volume growth, or 432 fbm/acre of saw-log volume growth per year for a 29-year period. On somewhat poorer sites in the Georgia Piedmont with a site index of 23 m (75 ft), annual growth has averaged 5.3 m³/ha (76 ft³/acre) or 319 fbm/acre over a 21-year period *(5,17,82,85,86)*.

In sapling stands, differences in growth rate of individual loblolly pines are evident at early ages when competition between trees begins. The growth differentiation process begins at earlier ages on better sites or at higher levels of stocking; it begins later on poor sites or at low levels of stocking *(51)*. The result is separation of trees into crown classes. Growth in height is a critical factor in the occupation of available space. Loblolly pine is a species in which individual trees tend to express dominance at an early age, and the most vigorous individuals that are best adapted to the microsite environment become dominants as the stand ages.

Faster growing trees develop larger live-crown ratios than do slower growing trees. Diameter growth of individual trees generally increases as crown surface area and crown ratio increase, with optimal diameter growth occurring when trees have at least a 40 percent live-crown ratio. Diameter increment does not occur uniformly on portions of the bole. Annual diameter growth is greatest within the crown and decreases with increased distance below the crown. This phenomenon causes the bole of loblolly pine trees to become cylindrical with increasing age (fig. 4). Height growth is not as sensitive as diameter growth to differences in crown size. Height

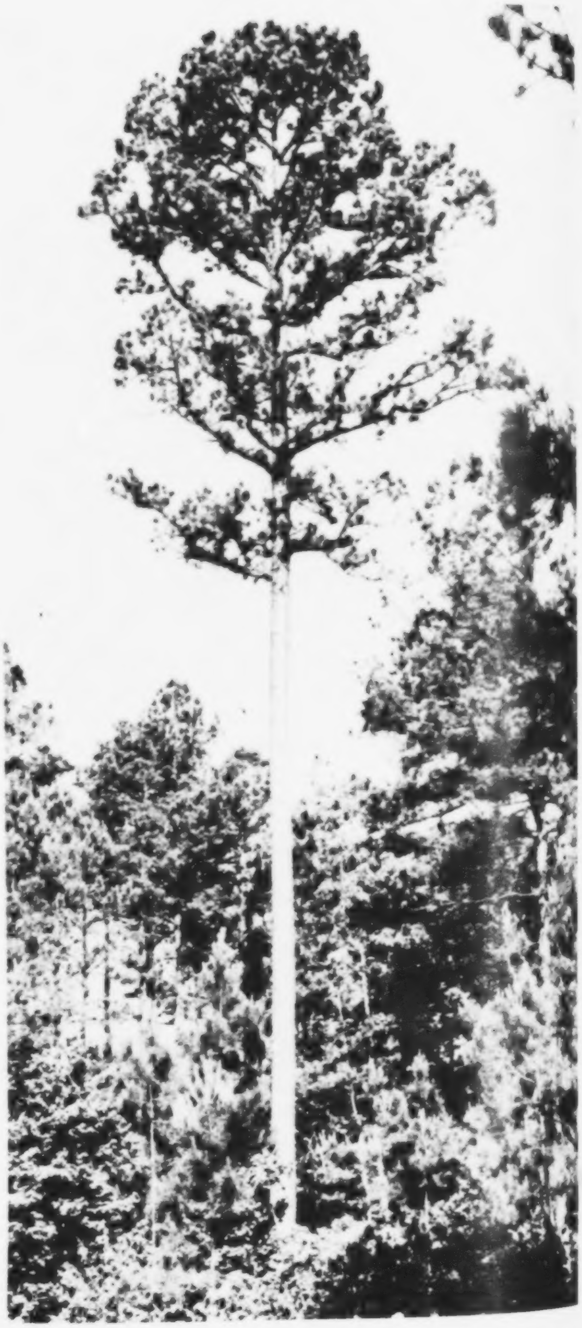

Figure 4—*A 61-cm (24-in) loblolly pine with three clear logs, on Crossett Experimental Forest, AR.*

growth of codominants is significantly less, however, in dense stands of trees with small crowns than in low-density stands of trees with larger crowns *(37,38,51)*.

Loblolly pine is a medium-lived tree. Maximum recorded age of one tree in a small stand of 20 trees in North Carolina was 245 years, with the group averaging 240 years. The largest tree in this stand was 135 cm (53 in) in d.b.h. and 45.7 m (150 ft) tall. Currently, the champion for the species in the "National Register of Big Trees" is located near Urania, LA, and is 143 cm (56.3 in) in d.b.h. and 49.7 m (163 ft) tall *(52)*.

Rooting Habit—The rooting habit of loblolly pine is strongly influenced by tree age, soil, and the soil environment. A young tree develops a short taproot but in most cases it ceases growth in favor of an extensive lateral-root system. A taproot 1.5 to 2.0 m (5.0 to 6.5 ft) long is often produced on deep, sandy or loamy soils. On heavy clay soils, the taproot tends to be stout and short. Taproots of loblolly pines are much smaller and shorter than those of shortleaf and longleaf pines. On excessively wet sites or when a water table or an impenetrable hardpan confines the roots to surface layers of soil, lateral roots are prominent in a superficial system *(3,50,108)*.

In a 6-year-old loblolly pine plantation in southeast Louisiana, 83 percent of total root weight was in the upper 46 cm (18 in) of soil. In a 31-year-old natural stand in North Carolina, the majority of the feeder roots less than 2.5 mm (0.1 in) in diameter were concentrated in the 15-cm (6-in) deep A horizon; practically no lateral roots were found below the 15- to 53-cm (6- to 21-in) depth of the B horizon *(14,59)*.

Roots of loblolly generally spread laterally farther than their crowns. As a result, root grafting is a common occurrence both in natural stands and closely spaced plantations. Roots grow at all times of the year, but most root growth occurs in April and May, and in late summer and early fall *(37,80,89,108)*.

Reaction to Competition—Loblolly pine is moderately tolerant when young but becomes intolerant of shade with age. Its shade tolerance is similar to that of shortleaf and Virginia pines, less than that of most hardwoods, and more than that of slash and longleaf pines *(31,37,108)*. Loblolly pine is most accurately classed as intolerant of shade.

Succession in loblolly pine stands that originate in old fields and cutover lands exhibit a rather predictable pattern. The more tolerant hardwoods (including various species of oaks and hickories, sweetgum, blackgum, beech, magnolia, holly, and dogwood) invade the understory of loblolly pine stands and, with time, gradually increase in numbers and in basal area. The hardwoods finally share dominance with each other and with loblolly pine *(37,83,100)*.

The climax forest for the loblolly pine type has been described as oak-hickory, beech-maple, magnolia-beech, and oak-hickory-pine in various parts of its range *(28,37)*. Others view the climax forest as several possible combinations of hardwood species and loblolly pine. There is evidence that within the range of loblolly pine several different tree species could potentially occupy a given area for an indefinite period of time and that disturbance is a naturally occurring phenomenon. If this is so, then the climax for this southern forest might best be termed the southern mixed hardwood-pine forest *(83)*.

Competition affects the growth of loblolly pine in varying degrees depending on the site, the amount and size of competing vegetation, and age of the loblolly pine stand. Across the southern region, average loss of volume production resulting from hardwood competition has been estimated at 25 percent in natural stands and 14 percent in plantations *(35)*. In a North Carolina study, residual hardwoods after logging reduced cubic-volume growth of a new stand of loblolly pine by 50 percent at 20 years, and where additional small hardwoods of sprout and seedling origin were present, growth was reduced by another 20 percent by age 20 *(10,64)*. Similar growth responses in young seedling and sapling stands have been observed in Arkansas, Louisiana, and Texas *(24,26,39)*. Although several short-term studies (5 years or less) of the effects of understory hardwoods on growth of older loblolly pine did not show measurable effects *(58)*, a long-term study (11 to 14 years) showed growth increases of 20 to 43 percent in cubic volume and 21 to 54 percent in board-foot volume after removal of understory vegetation *(39)*. Control of both residual overstory and understory hardwoods is a financially attractive silvicultural treatment for loblolly pine management *(10)*.

Silvicultural practices such as prescribed burns, the use of herbicides, and mechanical treatments arrest natural succession in loblolly pine stands by retarding the growth and development of hardwood understories. Prescribed fire is effective for manipulating understory vegetation, reducing excessive fuel (hazard reduction), disposing of logging slash, preparing planting sites and seedbeds, and improving wildlife habitat. Responses of the understory to prescribed fire varies with frequency and season of burning. Periodic winter burns keep hardwood understories in check, while a series of annual summer burns usually reduces vigor and increases mortality of hardwood rootstocks *(62)*. In the

Atlantic Coastal Plain, a series of prescribed burns, such as a winter burn followed by three annual summer burns before a harvest cut, has been more effective than disking for control of competing hardwood vegetation and improvement of pine seedling growth after establishment of natural regeneration *(103,104)*.

Loblolly pine expresses dominance early, and various crown classes develop rapidly under competition on good sites; but in dense stands on poor sites, expression of dominance and crown differentiation are slower *(37)*.

Dense natural stands of loblolly pine usually respond well to precommercial thinning. To ensure the best volume gains, stocking should be reduced to 1,235 to 1,730 stems per hectare (500 to 700/acre) by age 5. When managing for sawtimber, thinnings increase diameter growth of residual trees and allow growth to be put on the better trees in the stand, thus maximizing saw-log volume growth and profitability *(56,78)*.

Loblolly pines that have developed in a suppressed condition respond in varying degrees to release. Increases in diameter growth after release are related to live-crown ratio and crown growing space, but trees of large diameter generally respond less than trees of small diameter. Trees with well-developed crowns usually respond best to release. Trees long suppressed may also grow much faster in both height and diameter after release but may never attain the growth rate of trees that were never suppressed *(37,75)*.

Loblolly pine can be regenerated and managed with any of the four recognized reproduction cutting methods and silvicultural systems. Even-aged management is most commonly used on large acreages; however, uneven-aged management with selection cutting has proved to be a successful alternative.

Damaging Agents—Agents that cause periodic damage to individual trees or stands of loblolly pine include wind, lightning, temperature extremes, ice, drought, flooding, insects, and diseases. Voluminous literature about the effects of these agents in loblolly pine stands on a range of sites, soils, and stand conditions is available; a brief summary follows.

Large dominant trees usually are more vulnerable to high winds than smaller trees, and trees with large cankers caused by rust disease break more readily than sound trees. In general, damage resulting from severe winds associated with hurricanes or thunderstorms is caused primarily by windthrow or blowdown. Windthrow is most common on shallow soils with coarse-textured profiles. Wind damage is also more likely to occur in recently thinned stands *(37,105)*.

Direct losses to lightning are small, averaging only about 5 trees per 100 hectares (2/100 acres) per year. Large, dominant, open-grown trees are generally the most vulnerable to lightning strikes. Probably more important than the direct damage caused by lightning is the possibility that a lightning-struck tree will become a center for insect infestation *(37)*.

Damage or seedling mortality caused by low or freezing temperatures occurs primarily in the northern extremities of the loblolly pine range. Older, vigorous trees can usually withstand occasional low temperatures *(37,79)*. Greater damage frequently occurs from ice or glaze storms. This damage is normally associated with branch and stem breakage, severe bending and, in some cases, uprooting. Ice damage is usually more severe in recently thinned (particularly row thinned) plantations and in heavily stocked stands made up of slender, small-crowned trees *(37,91)*. Extremely high summer temperatures and drought often cause mortality of seedlings and, in some cases, of larger trees. Heat and drought more often cause stress and a resultant loss of vigor and growth in larger trees, which can lead to more serious problems with insect infestations.

Loblolly pine seedlings or saplings cannot withstand prolonged flooding. Complete inundation for more than 2 weeks during the growing season often results in significant mortality. Larger trees are classed as moderately tolerant of flooding; typically they can survive one season but usually succumb during the second growing season if continuously in 0.3 m (1 ft) or more of water *(37,113)*.

A comprehensive review of insects associated with loblolly pine is provided by Baker *(7)*. Loblolly pine serves as host to a multitude of insect pests; however, insect outbreaks vary greatly in frequency, area, and duration. The majority of outbreaks are small and short-lived and usually consist of only one or a few spots in a stand, but some may expand until they encompass hundreds of hectares and last for several years before subsiding. With only a few exceptions, the majority of the insects that attack loblolly pine are insignificant in terms of damage or mortality.

The most serious insect pests to loblolly pine are bark beetles, particularly the southern pine beetle *(Dendroctonus frontalis)*, whose attack may result in extensive mortality, and pine engraver beetles *(Ips* spp.), that can cause death of isolated or small groups of trees; pine tip moths *(Rhyacionia* spp.), that often infest young trees; seedling debarking weevils *(Hylobius* spp. and *Pachylobius* spp.), that sometimes result in girdling and death of young seedlings up to 13 mm (0.5 in) in d.b.h.; and cone and seed feeders (*Dioryctria* spp. and *Leptoglossus* spp.), that can seriously reduce seed crops. Loblolly pine is generally the preferred host of the southern pine beetle, which is the most destructive insect for this species *(102)*. Most infestations originate in stands that are under stress because of poor site, adverse weather, overstocking, or overmaturity. Once a buildup of southern pine beetle occurs, adjacent well-managed stands may also be attacked. Preventive measures include avoidance of planting offsite and maintenance of vigorous stands through silvicultural practices such as controlling density through thinning and harvesting trees at or before maturity *(6,102)*.

A general account of diseases associated with loblolly pine is provided by Hepting *(54)*. The most common disease problems in loblolly pine are related to seedling susceptibility to black root rot (*Fusarium* spp., *Macrophomina* spp., and possibly others) and fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*); sapling susceptibility to fusiform rust; root rot by *Heterobasidion annosum* in thinned stands; and heart rot in old stands with *Phellinus pini* in the bole and *Phaeolus schweinitzii* primarily in the butt.

Nursery seedlings are subject to root rot in soils with pH above 6.0 under moist conditions; however, root rot becomes severe only if soil temperatures remain above 32° C (90° F) for long periods. Fusiform rust is also a major nursery disease in many parts of the South, requiring rigid spray programs to keep infections low.

The most serious stem disease is fusiform rust, which kills and disfigures young trees from Virginia to Texas. Saplings and older trees, especially if planted, are subject to attacks by *Heterobasidion annosum* in stands where some cutting has taken place. It is considered a disease problem in plantation management second only to fusiform rust. Losses in natural stands or in the absence of some cutting are generally negligible.

Phaeolus schweinitzii causes a root and butt rot, usually after basal or root injuries, and in the Deep South it has caused more loss in some areas than *Heterobasidion annosum*. Red heart (*Phellinus pini*), entering almost entirely through dead branch stubs, is rarely a factor under the age of 60 years. However, when large branches that have heartwood begin to die, red heart can set in and destroy much of a tree.

Special Uses

Natural loblolly pine stands as well as intensively managed plantations provide habitat for a variety of game and nongame wildlife species. The primary game species that inhabit pine and pine-hardwood forests include white-tailed deer, gray and fox squirrel, bobwhite quail, wild turkey, mourning doves, and rabbits *(94)*. Some of these species utilize the habitat through all stages of stand development, while others are attracted for only a short time during a particular stage of development. For example, a loblolly pine plantation can provide forage for deer only from the time of planting to crown closure. Without modifying management practices, this usually occurs in 8 to 10 years *(13)*. Bobwhite tend to use the plantation until a decline in favored food species occurs *(20)*. As the habitat deteriorates, deer and quail usually move to mature pine or pine-hardwood forests *(47)* or to other newly established plantations. Management modifications such as wider planting spacing and early and frequent thinnings will delay crown closure, and periodic prescribed burns will stimulate wildlife food production.

Wild turkeys inhabit upland pine and pine-hardwood forests and do particularly well on large tracts of mature timber with frequent openings and where prescribed burning is conducted *(96,97)*.

Pine lands are the chief habitat for some birds such as the pine warbler, brown-headed nuthatch, and Bachman's warbler. Old-growth stands are very important to the existence of the red-cockaded woodpecker. Large loblolly pine trees are favorite roosting places for many birds and provide an important nesting site for ospreys and the bald eagle *(46)*.

In urban forestry, loblolly pines often are used as shade trees and for wind and noise barriers throughout the South. They also have been used extensively for soil stabilization and control of areas subject to severe surface erosion and gullying. Loblolly pine provides rapid growth and site occupancy and good litter production for these purposes *(114,115)*.

Biomass for energy is currently being obtained from precommercial thinnings and from logging residue in loblolly pine stands. Utilization of these energy sources will undoubtedly increase, and loblolly pine energy plantations may become a reality.

Genetics

Population Differences

Many studies of racial and geographical variation in loblolly pine have been carried out since research with loblolly pine began in the early part of this century. Provenance studies have shown differences in survival, growth, disease resistance, drought hardiness, and cold hardiness attributable to source of the seed. The many findings of geographical differences (some of which show continuous, others discontinuous variation with geographic location) have led geneticists to consider some differences to be racial. Although distinct races of loblolly pine have not been named and described, recommended zones for collecting seed for planting of seedlings in a given geographic area have been established. Seed orchards for producing seed for specific areas have been established *(29,30,111)*.

Resistance of certain families of loblolly pine to fusiform rust and the geographic variation in susceptibility of loblolly pine to the rust are important research findings now in use. Special rust-resistant seed orchards have been established with the most rust-resistant clones producing seed for specific geographic areas. Rust resistance of seedlings is low from seed sources in some areas such as east Texas and high for those in other areas such as Georgia and South Carolina. Rust resistance seems to be clinal and is strongly related to longitude of the seed source—the westerly sources are more resistant than the easterly ones *(30,109,117)*.

Loblolly pine from the Lost Pines area of east Texas is more drought resistant than those with more easterly seed sources. The use of drought-hardy strains of loblolly pine for planting in drought-prone areas is most important. Cold hardiness is also an important characteristic to be considered, especially if loblolly is to be planted north or inland of its natural range. As expected, the more northerly sources of loblolly pine are more cold resistant *(29,37)*.

Seed source affects yields of loblolly pine. These yield differences are usually attributable to the combined effects of seed source on survival, height and diameter growth, and susceptibility to fusiform-rust infection. Clinal effects in growth also are evident in the data, with trees from coastal areas growing faster than those from inland sources, except in northerly plantings. Loblolly pine trees within a seed source also vary in growth. Progeny tests of half-sib families (most of which are less than 10 years old) have shown significant differences in height growth with differences between races and families being additive. Nursery-bed selections of plus-seedlings have been effective in producing height growth gains for loblolly pine of 45 percent at age 10, and volume of the average plus-tree was 3.4 times that of the control. Although gains in other traits are not consistent, nursery-bed selection appears to be an effective first step in choosing fast-growing seedlings *(30,53,109,112)*.

Wood characteristics of loblolly pine have been extensively investigated. Specific gravity generally decreases from southeast to northeast and from the coastal areas to the Piedmont. Wide tree-to-tree variation also has been found for specific gravity, tracheid length, fiber angle, and cellulose type. A most important research result for geneticists has been that wood quality characteristics and growth rate at older ages are not highly correlated and, more important, not negatively correlated, which allows breeding for several traits *(30)*.

Hybrids

The best-known southern pine hybrid is Sonderegger pine *(Pinus* × *sondereggeri* H. H. Chapm.), a cross between longleaf and loblolly pine. This natural hybrid occurs quite frequently in Louisiana and east Texas. It is conspicuous in nursery beds and plantings of longleaf pine because the hybrid gains height growth in the first year in contrast to longleaf seedlings, which do not. Natural hybrids of pond and loblolly pine have been observed in North Carolina, and those of pond, loblolly, and pitch pine have been recognized and studied in New Jersey, Delaware, and Maryland *(37,87)*. Natural hybrids of loblolly and shortleaf are known to occur in Oklahoma and east Texas *(29,37,49)*, and based on observations of tree characteristics intermediate between loblolly and shortleaf, they probably also occur in Louisiana and Arkansas in areas where the two species commonly occur together. Hybridization between these two species is thought to contribute to the fusiform-rust resistance of loblolly pine from those sources *(29)*.

Artificial hybrids of loblolly pine and the other southern yellow pines have been produced. Two crosses—loblolly × shortleaf pine and loblolly × pitch pine—show considerable promise for use on a commercial scale. The loblolly × shortleaf cross will be used in areas with high fusiform-rust incidence for breeding a strain of loblolly pine resistant to the disease *(60)*. The loblolly × pitch cross has growth characteristics of loblolly pine and cold resistance of pitch pine, making the hybrid more suitable for plantings in the north *(30)*.

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Pinus virginiana Mill. Virginia Pine

Pinaceae Pine family

Katherine K. Carter and Albert G. Snow, Jr.

Virginia pine *(Pinus virginiana)* has a definite place among trees of commercial importance in spite of once being considered a "forest weed" and called scrub pine. Also known as Jersey pine and spruce pine, it does so well in reforesting abandoned and cutover lands that it has become a principal source of pulpwood and lumber in the southeast. Virginia pine is commonly a small or medium-sized tree but a record tree has been measured with 81 cm (31.8 in) in d.b.h. and 34.7 m (114 ft) in height.

Habitat

Native Range

Virginia pine (figs. 1, 2) generally grows throughout the Piedmont and at lower elevations in the mountains from central Pennsylvania southwestward to northeastern Mississippi, Alabama, and northern Georgia. It is also found in the Atlantic Coastal Plain as far north as New Jersey and Long

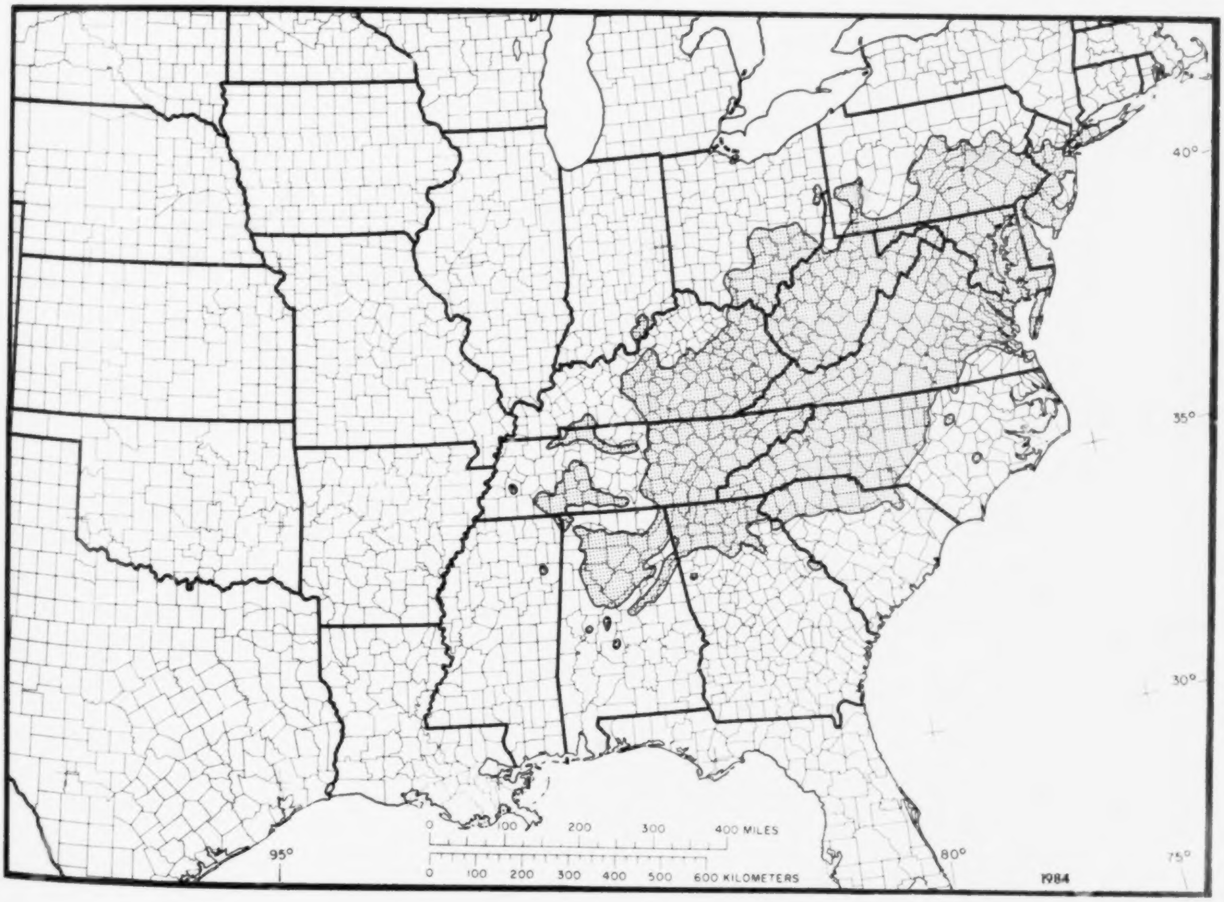

Figure 1—*The native range of Virginia pine.*

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Figure 2—*Virginia pine on the George Washington National Forest, VA.*

Island, NY, and extends westward in scattered areas into Ohio, southern Indiana, and Tennessee.

Climate

The annual precipitation in the native range of Virginia pine averages 890 to 1400 mm (35 to 55 in) and is fairly well distributed throughout the year. Rainfall generally is greatest in the southwestern portion of the range. The climate throughout most of this area is classified as humid.

Summer temperatures average about 21° to 24° C (70° to 75° F); winter temperatures range from –4°to 4° C (25° to 40° F); and the average number of frost-free days varies from more than 225 on the eastern and southern edge of the Piedmont to 160 days on the more mountainous areas to the west and north.

Soils and Topography

Virginia pine grows well on a variety of soils derived from marine deposits, from crystalline rocks, sandstones, and shales, and from limestone to a lesser extent. These are classified as Spodosols and Inceptisols. After harvesting or fire, these soils are subject to moderate sheet and gully erosion; erosion can become severe on shale soils. On many areas that now support Virginia pine, much of the A horizon is gone because of past erosion under intensive agricultural use.

The species grows best on clay, loam, or sandy loam; it generally does poorly on serpentine soils, shallow shaly soils, and very sandy soils. It thrives only in moderately well drained to well drained soils and is less tolerant of wet sites and impeded drainage than pitch and loblolly pines *(Pinus rigida* and *P. taeda).* Virginia pine generally tolerates soil acidities ranging from pH 4.6 to 7.9 *(39).* Soil beneath a Virginia pine stand was more acidic and contained more organic matter than soil under shortleaf *(P. echinata),* loblolly, or white *(P. strobus)* pine stands *(30).*

Virginia pine usually is found at elevations of 15 to 760 m (50 to 2,500 ft). It comes in freely on abandoned farmland throughout its range.

Associated Forest Cover

Virginia pine often grows in pure stands, usually as a pioneer species on old fields, burned areas, or other disturbed sites. It is a major species in the forest cover types Virginia Pine–Oak (Society of American Foresters Type 78) and Virginia Pine (Type 79) *(17).* It is an associate in the following cover types: Post Oak–Blackjack Oak (Type 40), Bear Oak (Type 43), Chestnut Oak (Type 44), White Oak–Black Oak–Northern Red Oak (Type 52), Pitch Pine (Type 45), Eastern Redcedar (Type 46), Shortleaf Pine (Type 75), Loblolly Pine (Type 81), and Loblolly Pine–Hardwood (Type 82).

Other than those named in the types, species that commonly grow with Virginia pine in various parts of its range are white oak *(Quercus alba),* southern red oak *(Q. falcata),* red maple *(Acer rubrum),* hickories *(Carya* spp.), blackgum *(Nyssa sylvatica),* sweetgum *(Liquidambar styraciflua),* eastern hemlock *(Tsuga canadensis),* Table Mountain pine *(Pinus pungens),* and eastern white pine *(P. strobus).*

In central Pennsylvania, two ground-cover types serve as indicators of site quality for Virginia pine. The flowering dogwood/clubmoss *(Cornus florida/Lycopodium)* type indicates the better site indexes ranging from 15.2 to 21.3 m (50 to 70 ft); the bear oak/reindeer moss *(Quercus ilicifolia/Cladonia)* type indicates average and poor site indexes between 9.1 to 15.2 m (30 and 50 ft) *(39)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Virginia pine is monoecious. Pollen shedding and female cone receptivity begin about the middle of March in the southern part of the species range, and as late as the latter part of May in the northern part. Virginia pine is wind pollinated and primarily outcrossing, though self-fertilization is possible. Fertilization takes place in early June some 13 months later, when the cones have nearly reached full size. Seeds become viable by middle to late August of the year after pollination but are difficult to extract before cone maturation, which occurs from late September to early November. Unlike many other pines, Virginia pine produces cones in all parts of the crown. Empty cones usually persist on the tree for several years and can remain for as many as 15 years.

Seed Production and Dissemination—Open-grown trees often produce cones as early as 5 years of age, and a few trees have been known to flower at 18 months *(3)*. In dense stands, cone production can be delayed for as many as 50 years. As stands become more open, cone production is accelerated *(36)*. Virginia pine produces some seed each year, with heavy cone crops occurring at intervals of 3 or more years. Good cone crops can be produced in 2 successive years, however, and peak seed years do not necessarily coincide throughout the range. Early cone production is under strong genetic control and can be increased by family selection or fertilization *(7,9)*.

Seed dispersal starts in October and is complete within 3 months, though some seeds may continue to be released until the following spring. Most of the seeds fall within 30 m (100 ft) of trees with an average height of 18 m (60 ft); however, stocking often is adequate at greater distances, particularly on the lee side of a seed source. In the coastal plain of Maryland, seedfall was measured on a 40-meter-wide (132 ft) strip cut through Virginia pine. Over a 4-year period, seedfall per hectare ranged from 15,800 to 98,800 (6,400 to 40,000/acre) *(18)*. The number of clean seeds per kilogram ranges from 100,750 to 200,800 (45,700 to 91,100/lb); the average is 122,100 (55,400/lb) *(35)*.

Seed and cone insects can severely reduce the yield of viable seed. Seed yields from cones from which insects were excluded by wire screens were twice as high as those from unprotected cones *(8)*. Major insect pests are two types of seedbugs: the shieldbacked pine seedbug *(Tetyra bipunctata)* and the southern pine seedbug *(Leptoglossus corculus)*. Several types of coneworms *(Dioryctria* spp.) and cone borers *(Eucosma* spp.) also infect Virginia pine. The Virginia pine sawfly *(Neodiprion pratti pratti)* and Nantucket pine tip moth *(Rhyacionia frustrana)* can destroy young conelets *(16)*.

Seedling Development—An exposed mineral soil seedbed is essential for successful establishment of seedlings. In one study area in the southern Appalachians, all regeneration of Virginia pine over a 120-year period was related to site disturbances by fires or logging *(1)*. Such site disturbance can result in two to four times as much germination as on undisturbed seedbeds, and 2-year survival that is four times as great *(41)*.

Exposing wet Virginia pine seeds to artificial light before sowing greatly increases germination. Maximum germination is obtained by exposing seeds that have been soaked in water for 24 hours to 30 minutes of red light. The stimulus to germination by this exposure can be reversed by treatment with far-red light *(39)*. Germination is epigeal *(35)*.

Seedlings require direct sunlight for best growth. Even partial shade reduces growth, and seedlings do not survive under full shade. Given adequate light and a good seedbed, however, several thousand seedlings per hectare can become established. Precommercial thinning at age 5 has been recommended to prevent stagnation in heavily stocked seedling stands *(11)*.

Virginia pine seedlings grown in containers in the greenhouse can be used to advance growth and cone production by 1 year compared to the use of bare-root stock *(6)*. Extra light from an incandescent source coupled with a high level of nutrition can quadruple height growth in one season. Long photoperiods also induce other effects such as increased internodal length, accelerated cycles of bud formation, and breaking of bud dormancy *(39)*.

The balance and relative abundance of inorganic elements in the soil solution also are important to the establishment and growth of Virginia pine. In basic nutrition studies in irrigated sand cultures, symptoms of deficiency appeared when either potassium or magnesium was supplied at 0.01 milliequivalent (meq) or less per liter. Amounts adequate for healthy height growth were 0.35 meq of calcium and 2 meq of magnesium per liter. The adequacy level for potassium was between 0.1 and 1 meq; the minimum levels for nitrogen and phosphorus were 1.78 and 0.03 meq, respectively *(39)*.

Virginia pine seedlings are more tolerant of low soil moisture than most other pines. Although they may survive when moisture is low, their rate of growth is slower on dry sites. Seedlings reach a height of 10 to 20 cm (4 to 8 in) in the first year when growth conditions are favorable. At the end of 10 years, the average height may reach 5 m (17 ft) on the better sites.

Many species of mycorrhizae representing nine genera (*Amanita, Boletus, Cenococcum, Gomphidius, Lepiota, Paxillus, Rhizopogon, Russula,* and *Scleroderma*) are known to form associations with the roots of Virginia pine *(23)*.

Vegetative Reproduction—Sprout growth on Virginia pine is rare. Occasionally, cut stubs produce a few short-lived sprouts from dormant buds. Rooting of cuttings from 7- and 8-year-old Virginia pine is most successful (72 percent rooted) when cuttings were taken in December and treated with 0.2 percent indolebutyric acid before being placed in a mist chamber *(40)*. Cuttings from 1-year-old seedlings also can be rooted, but those taken from mature trees fail to root *(25)*.

Grafting generally is about 65 percent successful when dormant scions are grafted onto dormant rootstock. The side-veneer graft technique is most commonly used, but other methods also are successful. Virginia pine grafts are more susceptible to mold than grafts of the other southern pines *(25)*.

Clonal plantlets can be obtained from tissue cultures when cotyledons from Virginia pine embryos are used. However, the rooting techniques necessary for commercial production of these plantlets have not yet been developed *(10)*.

Sapling and Pole Stages to Maturity

Growth and Yield—On average sites, well-stocked stands can have as many as 3,950 stems per hectare (1,600/acre) at 20 years of age. The number drops to about 500/ha (200/acre) in 70-year-old stands. The site index for Virginia pine is the average height of dominant trees measured at age 50 years. In North Carolina, the average merchantable volume per hectare for site index 18.2 m (60 ft) land is 112 m^3 (1,600 ft^3/acre) at 20 years and 354 m^3 (5,050 ft^3/acre) at 70 years *(36)*. Volumes for Maryland are intermediate between the higher values for North Carolina and the lower values for Pennsylvania. In a regional study extending from Maryland to South Carolina, merchantable volumes per hectare for fully stocked, pure, 60-year-old stands ranged from 155 m^3/ha (2,210 ft^3/acre) for site index 16.8 m (55 ft) land to 602 m^3/ha (8,600 ft^3/acre) for site index 24.4 m (80 ft) land *(31)*.

On the best sites, trees can reach a height of 37 m (120 ft) at maturity, but the average height ranges from 15 to 23 m (50 to 75 ft) at age 50. An annual growth rate of 6 m^3/ha (1 cord/acre) is possible over a large portion of its natural range.

Because Virginia pine is shallow rooted and subject to windthrow and to damage from ice and snow, thinning is not recommended in older stands. In one thinned 17-year-old stand the diameter growth of trees was 50 percent greater than that of controls; however, there was no overall stand response because of frequent windthrow in the thinned stand. Windthrow is not serious in younger stands, which can be thinned safely, but the growth response in these stands may not be sufficient to replace the volume removed by the thinning *(19)*.

Virginia pine planted on old fields grows well. One plantation in Iowa had a mean annual height growth of 0.6 m (1.9 ft) after 15 years. This growth was better than that of five other pine species planted on the same sites. The mean annual diameter growth was 8.6 mm (0.34 in) during the same period *(39)*. Plantations in the Cross Timbers area of Oklahoma survived well when moisture was adequate during the year of establishment *(32)*. In the Cumberland Plateau, planted Virginia pine on site index 21.2 m (70 ft) produced a merchantable volume of approximately 140 m^3/ha (2,000 ft^3/acre) at age 20 *(37)*.

In central Tennessee, Virginia pine outperforms shortleaf and loblolly pines on dry ridges and on warm slopes with shallow soil *(38)*. On these sites it is estimated to produce approximately 56 m^3 more per hectare (800 ft^3 or 4,000 fbm/acre) than shortleaf pine, on a 50-year rotation *(22)*. On good sites in the Piedmont or on cove sites in the southern Appalachians, however, growth of Virginia pine is inferior to the other southern pines. Natural pruning in Virginia pine is slow because the branches are resinous.

Rooting Habit—Virginia pine is a shallow-rooted species and losses from windthrow are likely to occur if old stands are thinned excessively *(5)*.

Reaction to Competition—Being intolerant of shade, Virginia pine is a transitional type and is eventually replaced by more tolerant hardwood species. It is a pioneer species, coming in after fire and on eroded areas or wornout old fields. Compared with associated pines, it is generally more successful on poorer sites. Virginia pine seedlings cannot become established under the shade of an existing stand, so hardwoods invade the understory. These hardwoods become dominant and gradually take over the area in succeeding generations, unless fire or other factors retard them *(39)*.

Damaging Agents—Heart rot due to *Phellinus pini* often is present in stands more than 60 years old, but it is rare in stands less than 50 years of age. In a severe case, as much as 34 percent of the trees in a 59-year-old stand were infected *(36)*. Partly because of its susceptibility to heart rot, pulpwood rotations generally are preferred to sawtimber rotations in Virginia pine.

The other serious disease of Virginia pine is pitch canker *(Fusarium moniliforme* var. *subglutinans)*, which enters twigs or stems through small wounds and causes a heavy exudation of pitch. The canker enlarges rapidly and eventually girdles the twig or stem. Seedlings infected with pitch canker have a mortality rate of about 90 percent *(15)*. Some variation in susceptibility to pitch canker appears to have a genetic basis *(2)*.

Other diseases usually cause little loss of growth in Virginia pine. Stem cankers *(Atropellis tingens)*, eastern gall rust *(Cronartium quercuum)*, a stem rust *(C. comptoniae)*, root rot *(Heterobasidion annosum)*, and butt rots *(Poria subacida, Phaeolus schweinitzii)* occasionally infest Virginia pine.

The principal forest insects that cause significant damage to Virginia pine are the southern pine beetle *(Dendroctonus frontalis)*, *Ips* spp., and pine sawflies, the Virginia pine sawfly *(Neodiprion pratti pratti)* and the redheaded pine sawfly *(N. lecontei)*. Trees under stress of lightning, fire, or logging injury are more susceptible to insect attack than sound healthy trees *(39)*.

The pales weevil *(Hylobius pales)*, which feeds on and often kills small seedlings of several pine species, can greatly reduce the regeneration of Virginia pine. Attacks are most likely on recently cutover areas where pine roots provide the food needed to build up a large larval population.

Girdling by meadow mice can cause considerable damage in young trees. In Tennessee, they have reportedly caused heavy mortality in 8- or 9-year-old plantations *(26)*. In Maryland and Iowa, they have shown a strong preference for Virginia pine over other pine species *(39)*.

Young Virginia pines are particularly vulnerable to fire because of their thin bark and their lack of longlived dormant buds at the base, along the bole, and in the crown. Fire reduces the Virginia pine component in stands where this species is mixed with pitch, shortleaf, or loblolly pines.

The species also is sensitive to several air pollutants. Of 18 pine species tested, Virginia pine was most sensitive to ozone; 69 percent of the seedlings suffered foliar damage. Polluted air containing sulfur dioxide and oxides of nitrogen also reduced terminal growth, with most damage occurring between the 4th and 13th weeks after budbreak. Dormant seedlings are resistant to ozone pollution *(14,33)*.

Special Uses

Of the southern conifers, Virginia pine is most preferred as a Christmas tree. If families with desirable traits are selected and appropriate cultural practices are used, marketable Christmas trees can be produced in as few as 3 years, although the usual rotation age for Virginia pine Christmas trees is 5 to 10 years *(4,24)*.

In the Eastern and Central States, Virginia pine performs well when planted on strip-mined sites. In a study in West Virginia, Virginia pine survived well, grew quickly, and encountered no serious pests 14 years after being planted on a mined site *(43)*. It is also a satisfactory species for the reclamation of spoil banks in the Southeast *(27)*.

Because the wood of older trees is frequently softened by fungal decay, Virginia pine provides nesting habitat for woodpeckers. Leaving old, decayed trees near the margins of clearcuts provides nesting sites *(13)*.

Genetics

Population Differences

Most of the variation in Virginia pine is attributable to differences among individual trees or stands rather than to geographic origin, though it is suspected that populations in the Talladega Mountains of central Alabama and on the deep sands of the mid-Atlantic Coast are distinct ecotypes *(25)*. A rangewide sample of 2,114 trees revealed no evidence of north–south or east–west trends in specific gravity (unextracted wood) *(12)*. In studies of six wood properties of mature Virginia pine in Kentucky and Tennessee, variation usually was greater within a stand than among stands. However, tracheid length increased from south to north within this region *(42)*. Progeny tests of trees from the same locations also revealed significant variation in monoterpene contant and in stem volume at age 5. This variation was attributable to difference among stands and among individual trees within stands *(29,34)*. These and other progeny tests indicate that tree improvement programs for Virginia pine can significantly improve the stem form and growth rate.

Seeds from local sources or from locations with a climate similar to that of the planting site generally produce trees with the best survival and growth rates. Seed from southern provenances produce fast-growing trees on southern sites, but southern trees grow slowly and suffer winter injury when planted in the north *(20,21)*.

Hybrids

Hybrids of Virginia pine and Ocala sand pine *(Pinus clausa* var. *clausa)* can be made under controlled conditions with either species as the seed parent. Controlled crosses of *P. virginiana* with jack pine *(P. banksiana)* and lodgepole pine *(P. contorta)* have not been successful *(25)*.

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Pseudotsuga macrocarpa (Vasey) Mayr **Bigcone Douglas-Fir**

Pinaceae Pine family

Philip M. McDonald

Distinct in appearance and conspicuous among its usually shorter associates, bigcone Douglas-fir (*Pseudotsuga macrocarpa*) provides contrast and variability to the southern California landscape. The wood of the species, although suitable for coarse lumber, is scarcely utilized because the trees are scattered and are more valuable for esthetics and watershed protection.

Because the taxonomic characteristics of bigcone Douglas-fir are similar to those of its northern "cousin," Douglas-fir, it was at least twice assigned to the genus *Abies*. Commonly, the species has been called hemlock, false hemlock, and desert fir. Colloquially, it is often referred to as bigcone-spruce, probably because its drooping lower branches, stiff needles, and upright cones remind the observer of the spruce tree. The species' accepted common name, bigcone Douglas-fir, stresses its *Pseudotsuga* lineage and the extraordinary size of its cones.

The species has been grown successfully outside the continental United States. It was unknown in Europe until the seedlings were raised at Bayfordbury, England, in 1910. Trees also have been reported growing in Sussex and North Ireland, where they reached heights of more than 18 m (60 ft) and crown spread of 12 m (40 ft) *(3)*.

Habitat

Native Range

The range of bigcone Douglas-fir (fig. 1) is about 217 km (135 mi) from north to south and about 338 km (210 mi) from east to west. Distribution of the species, in general, is confined to the Transverse and Peninsular Ranges of southern California. It is found on Mount Pinos, technically in the Tehachapi Mountains but considered transitional between them and the Transverse Ranges. Northern limits are near Mount Pinos in Kern County, and the headwaters of Labrea Creek in Santa Barbara County. Westernmost limits are Mission Canyon in the Santa Ynez Mountains, and Zaca Peak in the San Rafael Mountains. Older publications claimed that bigcone Douglas-fir grew in central Baja California, Mexico; a more recent publication verifies that it does not *(11)*. The southern limit of the species is near Julian, San Diego County.

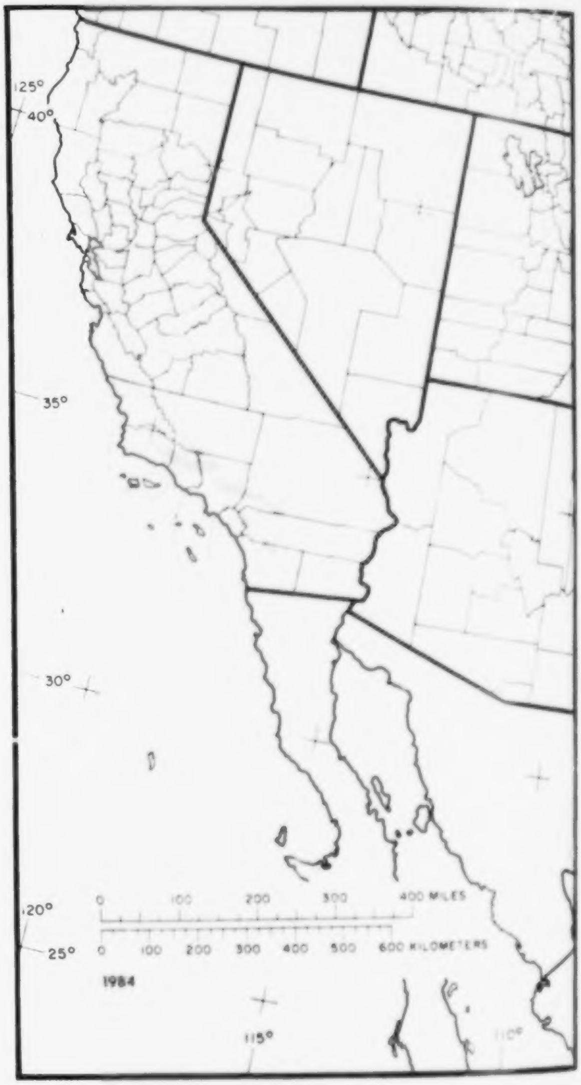

Figure 1—*The native range of bigcone Douglas-fir.*

Climate

The bigcone Douglas-fir habitat has long hot summers and cool moist winters. Extremes of annual

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precipitation vary from less than 250 mm (10 in) to 1270 mm (50 in), with 510 to 1020 mm (20 to 40 in) more common. The 30-year average at 1325 m (4,350 ft) elevation on a north aspect in the San Gabriel Mountains near Glendora, CA, was 610 mm (24 in). The lowest annual precipitation recorded was 250 mm (9.9 in) and the highest 1240 mm (49 in).

Snowpacks persist rarely in the range of the species, except at high elevations. Snow may fall, however, as early as October, or as late as May. During the rainy season, fog has been reported to add to the moisture available for tree growth *(14,15)*. During the summer, thunderstorms, hailstorms, or cloudbursts are common on higher mountains. Because much of this precipitation quickly evaporates, it does not foster tree growth *(15)*.

Specific temperature data within the range of bigcone Douglas-fir have not been reported other than for one station at 730-m (2,400-ft) elevation in the San Gabriel Mountains. The 22-year average mean for November through April was 9° ± 2° C (49° ± 3.7° F). Highs of above 27° C (80° F) and lows of below freezing were recorded in each of the 6 months. Annual temperatures at low to middle elevations in the mountain ranges of southern California where bigcone Douglas-fir grows seldom exceed 41° C (106° F) or drop below −12° C (10° F).

Soils and Topography

Soils on which bigcone Douglas-fir grows are derived from a wide variety of parent materials. Of 16 stands sampled throughout the range of the species, 4 grew on metasedimentary parent materials (sandstone and schist), 10 on granitics, and 2 in contact zones where the parent material was primarily granitic. The soil orders where bigcone Douglas-fir is most frequently found are Inceptisols and occasionally Alfisols. Soil series on metasedimentary material are probably Laughlin and Friant; in contact zones, Oak Glen; and on granitics, Tollhouse, Cieneba, Crouch, and two others that resemble Tish Tang and Neuns. Soils show a broad range of depth and development *(7)*. Some are shallow and poorly developed; others are deeper and better developed. Many are droughty. Bigcone Douglas-fir is capable of becoming established on soils too dry for other conifers.

Topography where the species is found is variable. Much of the terrain is rough and steep, strongly dissected by permanent and ephemeral streams. Slopes vary from 1 to 93 percent. Some stands occupy precipitous slopes of sheltered canyons, others are found on mostly steep broken slopes intermixed with cliffs and avalanche chutes, and still others thrive on gentler slopes and level ground. For all stands in the Santa Ana Mountains, average angle of slope is 34.5 degrees *(1)*. The species is well represented on all aspects, north slopes in particular.

Elevations of the bigcone Douglas-fir habitat range from 275 m (900 ft) on cool moist north slopes of canyon bottoms to 2400 m (7,875 ft) on warm south-facing plateaus. As elevations increase, the aspect best suited to bigcone Douglas-fir shifts from cooler to warmer. Many combinations of slope, aspect, soil, and elevation, therefore, support bigcone Douglas-fir.

Associated Forest Cover

Bigcone Douglas-fir has been listed in at least three vegetation classifications. One author placed the species in the California Coast Range forest, considering it an endemic and relic species. Another suggested that, in the San Bernardino Mountains at least, bigcone Douglas-fir was a member of the Live Oak Woodland and the Bigcone Douglas-fir vegetation types *(4)*. Among forest cover types, bigcone Douglas-fir is listed as a common associate in Canyon Live Oak (Society of American Foresters Type 249) *(5)*.

Bigcone Douglas-fir occupies an intermediate position between the lower elevation chaparral zone and the higher elevation mixed-conifer forest. It ranges downward into the chaparral as far as moisture conditions permit, and upward among the pines and firs as far as severe climate allows. Bigcone Douglas-fir does not extend solidly between the two types, however. The species is found in patches, in groups, and as single trees scattered among the oaks and chaparral. The continuity of stands also is broken by cliffs, slides, and areas of adverse soil.

Evidence suggesting that bigcone Douglas-fir has long occupied its present natural range is available from the fossil record. A likely progenitor of the species has been found in both the Pliocene and Pleistocene epochs *(6)*.

Fire, or its absence, greatly influences the extent and makeup of bigcone Douglas-fir stands. In general, repeated fires kill bigcone Douglas-fir, leaving only oaks or chaparral. Less frequent, but more catastrophic fires limit bigcone Douglas-fir to scattered large trees. When fires are infrequent, stands with several size and age classes develop; when fires are absent, multiaged stands having at least some regeneration evolve *(7)*.

In recent large fires in the eastern Transverse Range, nearly 60 percent of the trees escaped defoliation and 15 percent sprouted later, for a survival rate of 75 percent. Trees appear to have survived primarily because they were growing with large tree-size canyon live oaks *(Quercus chrysolepis)*, and in rough, broken terrain. Large canyon live oaks apparently act as a buffer against severe combustion characteristics of the chaparral nearby, and rough terrain impedes the speed and intensity of a conflagration. Survival of bigcone Douglas-fir on slopes of less than 20 degrees was only 37 percent. On slopes greater than 40 degrees, survival was more than 90 percent *(10)*.

Throughout its natural range, bigcone Douglas-fir is almost inseparable from canyon live oak. They form a community that is remarkably stable, self-perpetuating, somewhat exclusive, and probably climax in terms of succession. In the future, only minor shifts in species composition within the community are likely *(7)*.

In addition to canyon live oak, other tree associates, particularly at high elevations, are ponderosa pine *(Pinus ponderosa* var. *ponderosa)*, Jeffrey pine *(P. jeffreyi)*, singleleaf pinyon *(P. monophylla)*, and sugar pine *(P. lambertiana)*, incense-cedar *(Libocedrus decurrens)*, and California white fir *(Abies concolor* var. *lowiana)*. At middle elevations, tree associates are Coulter pine *(Pinus coulteri)*, Digger pine *(P. sabiniana)*, California black oak *(Quercus kelloggii)*, two-petal ash *(Fraxinus dipetala)*, and California-laurel *(Umbellularia californica)*. Singleleaf pinyon and knobcone pines *(Pinus attenuata)*, as well as curlleaf *(Cercocarpus ledifolius)* and birchleaf mountain-mahogany *(C. betuloides)* also are locally present. At lower elevations bigcone Douglas-fir, along with bigleaf maple *(Acer macrophyllum)* and white alder *(Alnus rhombifolia)*, is found in riparian settings, often in deep ravines, where it escapes fire. Coast live oak *(Quercus agrifolia)*, toyon *(Heteromeles arbutifolia)*, California scrub oak *(Quercus dumosa)*, birchleaf mountain-mahogany, laurel sumac *(Rhus laurina)*, sugar sumac *(R. ovata)*, and occasionally southern California walnut *(Juglans californica)* are associates of bigcone Douglas-fir *(3)* at lower elevations, mostly in nonriparian settings.

Many woody shrubs are found with bigcone Douglas-fir (table 1). At middle and high elevations, although scarce beneath bigcone Douglas-fir and canyon live oak crowns, they flourish in open spaces between trees or on edges of thickets. At low elevations, shrubs become abundant and well developed around scattered large firs.

A number of herbaceous species are scattered beneath bigcone Douglas-fir trees. Plants are relatively scarce and small because necessary nutrients, moisture, and light, already captured by the taller and deeper-rooted species, often are not available.

Table 1—Principal shrub associates of bigcone Douglas-fir in three elevational zones

Elevation	Scientific name	Common name
274 to 1067 m or 900 to 3,500 ft	*Adenostoma fasciculatum*	Chamise
	Artemisia californica	California sagebrush
	Ceanothus leucodermis	Chaparral whitethorn
	C. spinosus var. *palmeri*	Greenbark ceanothus
	Dendromecon rigida	Bush poppy
	Eriogonum fasciculatum	California buckwheat
	Salvia spp.	White sage
	Yucca whipplei	Chaparral yucca
1097 to 1676 m or 3,600 to 5,490 ft	*Adenostoma sparsifolium*	Red shanks
	Arctostaphylos glauca	Bigberry manzanita
	A. patula	Greenleaf manzanita
	Ceanothus cuneatus	Wedgeleaf ceanothus
	C. integerrimus	Deerbrush
	C. leucodermis	Chaparral whitethorn
	C. oliganthus	Hairy ceanothus
	C. spinosus var. *palmeri*	Greenbark ceanothus
1707 to 2438 m or 5,600 to 7,900 ft	*Arctostaphylos glauca*	Bigberry manzanita
	A. patula	Greenleaf manzanita
	Castanopsis sempervirens	Sierra chinkapin
	Ceanothus crassifolius	Hoary-leaf ceanothus
	C. cuneatus	Wedgeleaf ceanothus
	Chrysothamnus nauseosus	Rubber rabbitbrush
	Penstomon ternatus	Scarlet beardtongue
	Rhamnus californica	California buckthorn
	R. crocea	Hollyleaf buckthorn

Life History

Reproduction and Early Growth

Flowering and Fruiting—Throughout most of its natural range, bigcone Douglas-fir flowers from early March through mid-April. Male flowers generally shed pollen before female flowers become receptive—a mechanism that facilitates cross-pollination and prevents selfing. The plant is monoecious. Pollination in a given locality lasts 2 to 3 weeks. Fertilized conelets begin to enlarge in mid-July and are easily seen soon after.

Cones generally begin to dry and turn brown in August or September and most seed is released in September and October. Seeds are large and heavy and each has a rounded wing about 13 mm (0.5 in) long. Mature cones are rich dark brown and range from 11 to 17 cm (4 to 7 in) long. Some cones fall during winter, but others remain on the tree for at least a year.

Seed Production and Dissemination—Cone crops of bigcone Douglas-fir usually are small. Bumper crops are infrequent. Small amounts of seed, however, are borne on a few trees nearly every year. The minimum cone-bearing age of the species is about 20 years, but cones are rare on trees younger than 40 years. Most seeds fall beneath tree crowns and only during high winds is wider dissemination possible.

Insect larvae destroy some seeds in each cone crop and, at times, most of the crop. Rodents and birds consume seeds and aid in dispersal by distributing them beyond existing stands. Deer mice, chipmunks, ground squirrels, and the western gray squirrel eat large amounts of available seeds. The squirrels often bury seeds; some of these escape notice and eventually germinate.

Seedling Development—Natural seedbed requirements for germination are broad. Seeds of bigcone Douglas-fir have been observed to germinate successfully on the bare mineral soils of rocky outcrops and geomorphically active areas. They also germinate well in deep litter, usually beneath an overstory of oak and bigcone fir, but heavy losses from damping-off fungi often take their toll of tiny seedlings in this environment. Germination is epigeal.

Time of germination varies with elevation. In the chaparral zone, germination begins in late March. At higher elevations, germination ends in late May, or occasionally, early June.

Seed quality tends to be poor, as indicated in such early descriptions as "large number imperfect" and "a considerable percentage not fertile" *(14,15)*. In a laboratory test of seed stratified for 28 days in moist vermiculite with a day temperature of 30° C (86° F) and night temperature of 20° C (68° F), 31 percent of seeds germinated.

Weather, especially rainfall, can be critical to germination and early abundance of bigcone Douglas-fir seedlings. In the Santa Ana Mountains, 24,700 seedlings per hectare (10,000/acre) were present after a rainy period preceded by a year of above-average precipitation. The seedling environment, however, was not reported. New seedlings were absent during dry years *(1)*.

Bigcone Douglas-fir does not reproduce in stands having frequent fires, nor do badly damaged stands seed back to bigcone Douglas-fir, except during a series of wet years after a severe fire. Infertile seed, destruction of seed by fire, consumption of seed by birds and rodents, and lack of suitable microsites are possible reasons for scanty reproduction. Lack of shade could be another reason. Throughout its range, bigcone Douglas-fir reproduces most abundantly in locales undisturbed for at least 50 years, especially if shaded by canyon live oak trees. Where present, seedlings ranged in density from 140 to 1,030/ha (56 to 416/acre), with an average of 330/ha (132/acre). Advance reproduction, plants smaller than 2.5 cm (1.0 in) in d.b.h., was similar in mean and range of density *(7)*.

Artificial regeneration of bigcone Douglas-fir began in 1905, with outplantings in Los Angeles County. Survival was about 1 percent. The species was planted extensively (9,880 seedlings per hectare or 4,000/acre) for watershed rehabilitation from 1925 to 1930 by the Los Angeles County Forestry Department. From 1953 to 1975, this Department outplanted some bigcone Douglas-firs in all but 4 years *(13)*. Survival, unfortunately, is unknown.

Additional information on artificial regeneration of bigcone Douglas-fir is scanty. One small trial took place on a harsh site in Shasta County. Seed was germinated in a greenhouse in 1.9-liter (0.5-gal) milk cartons and 20 seedlings were outplanted as plugs when 1 year old. After five growing seasons in the field, survival was 65 percent and height averaged 53 cm (21 in) with a range of 18 to 76 cm (7 to 30 in).

Early height growth of bigcone Douglas-fir seedlings is slow, especially in deep shade. The species develops a taproot in early years, possibly at the expense of shoot growth.

Vegetative Reproduction—Bigcone Douglas-fir does not sprout from the root crown after cutting or fire. It has been propagated by grafting.

Sapling and Pole Stages to Maturity

Growth and Yield—In deep shade, growth of bigcone Douglas-fir seedlings and saplings is suppressed severely. Saplings may be only 60 cm (24 in) tall when 40 to 50 years old *(10)*. Growth rings often are indistinguishable. Bigcone Douglas-fir trees break through the oak overstory when 4 to 9 m (13 to 30 ft) tall and 40 to 70 years old. Breast-height diameter at this age ranges from 10 to 20 cm (4 to 8 in). Once above the oak foliage and into sunlight, growth of bigcone Douglas-fir accelerates. Annual height increment may exceed 30 cm (12 in).

In more open stands, bigcone Douglas-fir seedlings and saplings develop more quickly. Height of saplings may average 1 to 3 m (3 to 10 ft) at age 20 and from 4 to 15 m (13 to 50 ft) at age 40. From 40 to 100 years, annual increments of height and diameter may be uniform, even though amounts of annual precipitation vary. Trees in favorable growing condi-

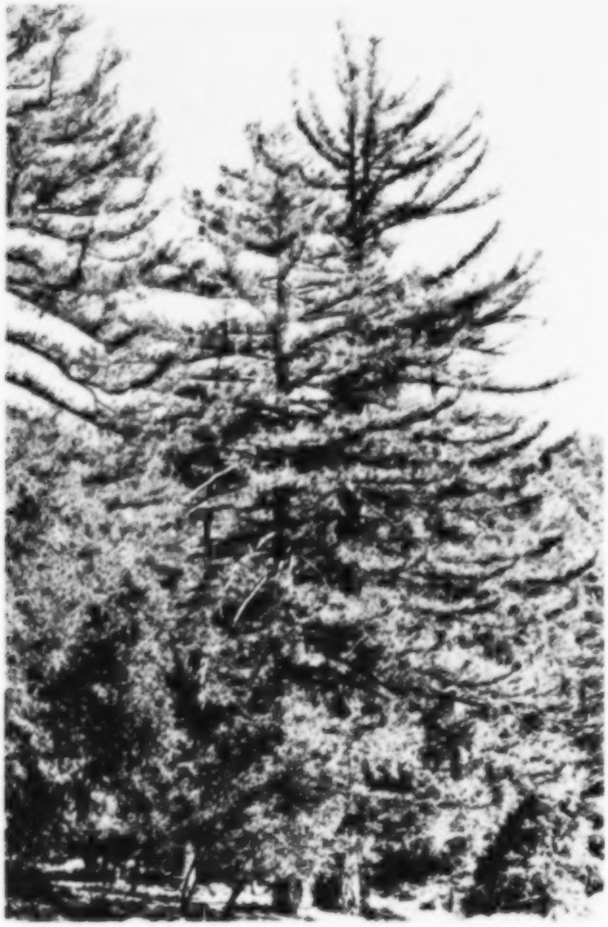

Figure 2—*Typical form and crown of bigcone Douglas-fir on a site of good quality, Angeles National Forest, CA. (Courtesy Edward E. Littrell, Sacramento, CA)*

tions often produce thick tapering boles and long drooping branches (fig. 2).

In the Santa Ana Mountains, diameter growth rates seem to be correlated to steepness of slope, with the average diameter of trees of a given age increasing as the angle of slope decreases. The largest trees of a given age, therefore, grow on level sites. The average d.b.h. of 20-year-old trees on level ground was 20 cm (7.8 in), but only 6 cm (2.2 in) on 60 to 90 degree slopes. A possible explanation of the difference is that little, if any, soil and litter are found on steep slopes, and water holding capacity and nutrients usually are low *(1)*.

Tree heights are affected by many variables, especially position on the slope. Trees generally are tallest at the base of slopes and shortest near the ridgeline. Trees at base of slopes commonly are straight and tall, averaging 24 to 30 m (80 to 100 ft) in height, but trees on upper slopes more often are gnarled and branchy and only 9 to 15 m (30 to 50 ft) tall.

The lifespan of bigcone Douglas-fir is as long as its coniferous associates, or longer. In the Santa Ana Mountains, trees 250 or more years old are commonplace. The oldest tree sampled was 622 years old and 140 cm (55 in) in d.b.h. A 157-cm (62-in) d.b.h. monarch of indeterminate age is nearby *(1)*. The largest living bigcone Douglas-fir grows near San Antonio Canyon on the Angeles National Forest in southern California. At 231 cm (91 in) in d.b.h. and 44.2 m (145 ft) in height, this tree deserves its name "Old Glory."

Bigcone Douglas-fir is well known for its ability to grow a new crown after severe burning. This ability has helped to sustain the species in its present natural range. New tissue, which leads to new branches, develops from the upper surface of defoliated limbs in the upper portions of the tree. Large sawtimber-sized trees, therefore, can develop new crowns, but seedlings, saplings, and overmature sawtimber usually cannot.

Boles also produce new shoots after fire, mechanical, or physiological injury. Vigorous intermediate-aged trees are particularly noted for this capability. In the Santa Ana Mountains, new shoots developed in trees that were from 13 to 114 cm (5 to 45 in) in d.b.h. and from 25 to 300 years old *(1)*.

Rooting Habit—The species is described as having a strong spreading root system.

Reaction to Competition—In its seedling stage, bigcone Douglas-fir requires at least some shade. In moist sheltered situations, however, it reproduces successfully in the open. Saplings and small poles need increasing amounts of light for best development. Mature trees usually are found in open stands, probably as a consequence of having adequate light and moisture. In general, bigcone Douglas-fir may be classed as intolerant of shade.

Damaging Agents—Fire is the most injurious agent of bigcone Douglas-fir. In spite of its ability to develop new crowns after complete defoliation (fig. 3), and its thick bark (15 to 20 cm or 6 to 8 in for trees more than 100-cm or 40-in d.b.h.), trees die from fire, and particularly from repeated fires that deplete energy reserves and enlarge old wounds.

Damage by insects and disease is not reported. The California flatheaded borer *(Melanophila californica)* has been observed in the wood of a few trees. Even

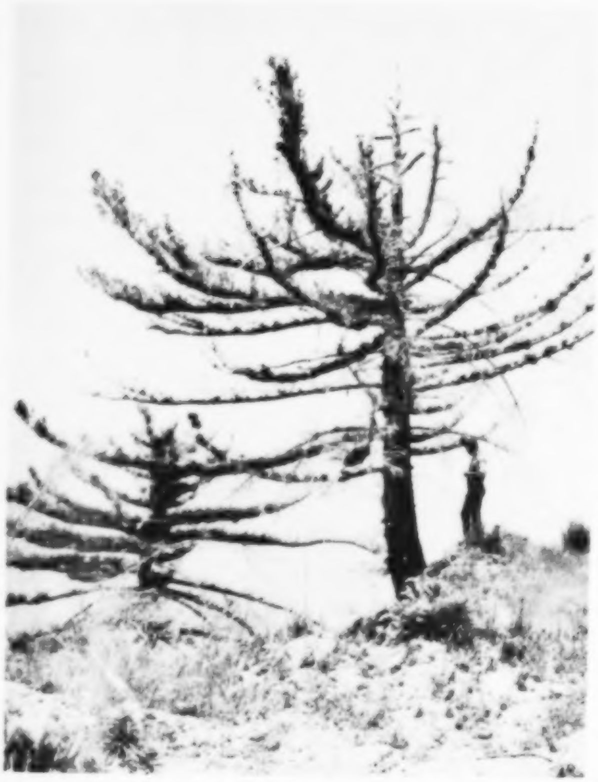

Figure 3—*New branches are developing on the upper parts of burned branches in this large bigcone Douglas-fir on the Angeles National Forest, CA.*

trees damaged by fire seem free of bark beetle attacks. A hard pitchy wood is given as a possible reason for lack of damage from these agents. A needle-cast fungus *(Rhabdocline pseudotsugae)* has been observed on bigcone Douglas-fir needles *(8)*. Older trees occasionally lose most of their needles, apparently from a physiological disorder, but epicormic branching along the bole usually replaces the lost crown. Damage to needles from ozone is another potential injury. However, in a sensitivity study, seedlings of bigcone Douglas-fir ranked low (11th of 13 conifer species and hybrids) in susceptibility to ozone injury *(9)*.

Many species of animals are associated with bigcone Douglas-fir, especially deer, rabbits, and woodrats. Browsing of seedlings is a major damage. Bigcone Douglas-fir stands are preferred spring habitat for black bears in the San Bernardino Mountains *(12)*. After the sapling stage, animal damage is negligible.

Special Uses

The wood of bigcone Douglas-fir is heavy, hard, and close grained, but not durable *(15)*. It has less sapwood than heartwood, the latter containing pockets of resin. In the past, bigcone Douglas-fir was used locally for fuel and to a small extent for coarse lumber. Currently, it has value in watersheds and wildlife habitats for its scenic beauty.

Genetics

Varieties or natural hybrids of bigcone Douglas-fir are not known, but an artificial cross of bigcone Douglas-fir and coast Douglas-fir was achieved in 1956 at Oregon State University, Corvallis. Hybrid seedlings indicated low mortality, good height growth, and a dense fibrous root system. They showed promise for outplanting on drier sites in the Douglas-fir region *(2)*.

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Pseudotsuga menziesii (Mirb.) Franco **Douglas-Fir**

Pinaceae Pine family

Richard K. Hermann and Denis P. Lavender

Douglas-fir *(Pseudotsuga menziesii)*, also called red-fir, Oregon-pine, Douglas-spruce, and piño Oregon (Spanish), is one of the world's most important and valuable timber trees. It has been a major component of the forests of western North America since the mid-Pleistocene *(30)*. Although the fossil record indicates that the native range of Douglas-fir has never extended beyond western North America, the species has been successfully introduced in the last 100 years into many regions of the temperate forest zone *(31)*. Two varieties of the species are recognized: *P. menziesii* (Mirb.) Franco var. *menziesii*, called coast Douglas-fir, and *P. menziesii* var. *glauca* (Beissn.) Franco, called Rocky Mountain or blue Douglas-fir.

Habitat

Native Range

The latitudinal range of Douglas-fir (fig. 1) is the greatest of any commercial conifer of western North America. Its native range, extending from latitude 19° to 55° N., resembles an inverted V with uneven sides. From the apex in central British Columbia, the shorter arm extends south along the Pacific Coast Ranges for about 2200 km (1,367 mi) to latitude 34° 44'N., representing the range of the typical coastal or green variety, *menziesii*; the longer arm stretches along the Rocky Mountains into the mountains of central Mexico over a distance of nearly 4500 km (2,796 mi), comprising the range of the other recognized variety, *glauca*—Rocky Mountain or blue. Nearly pure stands of Douglas-fir continue south from their northern limit on Vancouver Island through western Washington, Oregon, and the Klamath and Coast Ranges of northern California as far as the Santa Cruz Mountains. In the Sierra Nevada, Douglas-fir is a common part of the mixed conifer forest as far south as the Yosemite region. The range of Douglas-fir is fairly continuous through northern Idaho, western Montana, and northwestern Wyoming. Several outliers are present in Alberta and the eastern-central parts of Montana and Wyoming, the largest being in the Bighorn Mountains of Wyoming. In northeastern Oregon, and from southern Idaho south through the mountains of Utah, Nevada, Colorado, New Mexico, Arizona, extreme western Texas, and northern Mexico, the distribution becomes discontinuous (fig. 1).

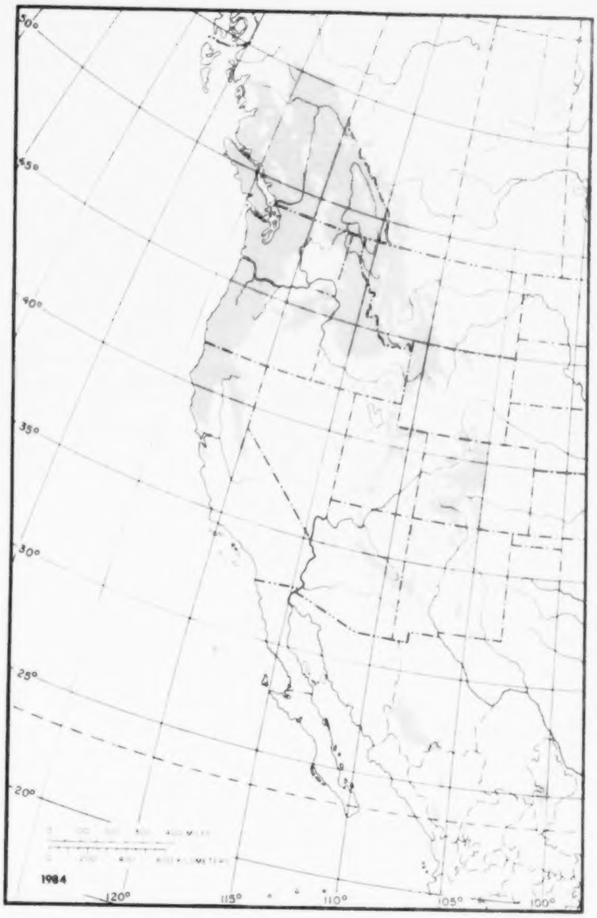

Figure 1—*The native range of Douglas-fir.*

Climate

Douglas-fir grows under a wide variety of climatic conditions (table 1). The coastal region of the Pacific Northwest has a maritime climate characterized by mild, wet winters and cool, relatively dry summers, a long frost-free season, and narrow diurnal fluctuations of temperature (6° to 8° C; 43° to 46° F).

The authors are Professor of Forest Ecology (retired), Oregon State University, Corvallis and Department Head, Faculty of Forestry, University of British Columbia, Vancouver.

Table 1—Climatic data for five regional subdivisions of the range of Douglas-fir *(6,62)*

Region	Mean temperature		Frost-free period	Mean precipitation	
	July	January		Annual	Snow fall
	°C	*°C*	*days*	*mm*	*cm*
Pacific Northwest					
Coastal	20 to 27	–2 to 3	195 to 260	760 to 3400	0 to 60
Cascades and Sierra Nevada	22 to 30	–9 to 3	80 to 180	610 to 3050	10 to 300
Rocky Mountains					
Northern	14 to 20	–7 to 3	60 to 120	560 to 1020	40 to 580
Central	14 to 21	–9 to –6	65 to 130	360 to 610	50 to 460
Southern	7 to 11	0 to 2	50 to 110	410 to 760	180 to 300
	°F	*°F*	*days*	*in*	*in*
Pacific Northwest					
Coastal	68 to 81	28 to 37	195 to 260	34 to 134	0 to 24
Cascades and Sierra Nevada	72 to 86	15 to 28	80 to 180	24 to 120	4 to 120
Rocky Mountains					
Northern	57 to 68	19 to 28	60 to 120	22 to 40	16 to 230
Central	57 to 70	16 to 22	65 to 130	14 to 24	20 to 180
Southern	45 to 52	32 to 36	50 to 110	16 to 30	70 to 120

Precipitation, mostly as rain, is concentrated in the winter months. Climate in the Cascade Range and Sierra Nevada tends to be more severe.

Altitude has a significant effect on local climate. In general, temperature decreases and precipitation increases with increasing elevation on both western and eastern slopes of the mountains. Winters are colder, frost-free seasons are shorter, and diurnal fluctuations of temperature are larger (10° to 16° C; 50° to 61° F). Much of the precipitation is snow. In the northern Rocky Mountains, Douglas-fir grows in a climate with a marked maritime influence. Mild continental climate prevails in all seasons, except midsummer. Precipitation is evenly distributed throughout the year, except for a dry period in July and August. In the central Rocky Mountains, the climate is continental. Winters are long and severe; summers are hot and in some parts of the region, very dry. Annual precipitation, higher on the western sides of the mountains, is mainly snow. Rainfall patterns for the southern Rocky Mountains generally show low winter precipitation east of the Continental Divide but high precipitation during the growing season. West of the Continental Divide, the rainfall is more evenly divided between winter and summer. Frost may occur in any month in the northern part of the range. Length of frost-free periods, however, varies within the central and southern Rocky Mountain regions, even at the same elevations.

Soils and Topography

The variety *menziesii* of Douglas-fir reaches its best growth on well-aerated, deep soils with a pH range from 5 to 6 (fig. 2). It will not thrive on poorly drained or compacted soils. Soils in the coastal belt of northern California, Oregon, and Washington originated chiefly from marine sandstones and shales with scattered igneous intrusions. These rocks have weathered deeply to fine-textured, well-drained soils under the mild, humid climate of the coast. Surface soils are generally acid, high in organic matter and total nitrogen, and low in base saturation. Soils in the Puget Sound area and in southwestern British Columbia are almost entirely of glacial origin. Soils farther inland within the range of the variety *menziesii* are derived from a wide variety of parent materials. These include metamorphosed sedimentary material in the northern Cascades and igneous rocks and formations of volcanic origin in the southern Cascades.

Depth of soils ranges from very shallow on steep slopes and ridgetops to deep in deposits of volcanic origin and residual and colluvial materials. Texture varies from gravelly sands to clays. Surface soils are in general moderately acid. Their organic matter content varies from moderate in the Cascade Range to high in portions of the Coast Range and Olympic Peninsula. Total nitrogen content varies considerably but is usually low in soils of glacial origin. Great soil

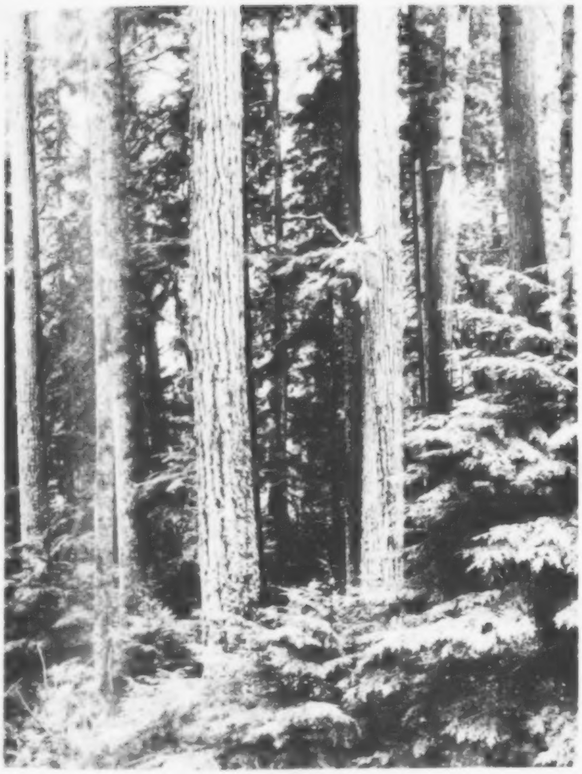

Figure 2—*Dense stand of Douglas-fir, nearly pure, in Pierce County, WA.*

groups characteristic of the range of coastal Douglas-fir include Haplohumults (Reddish Brown Lateritics) of the order Ultisols, Dystrochrepts (Brown Lateritics), Haplumbrepts (Sols Bruns Acides) of the order Inceptisols, Haplorthods (Western Brown Forest soils) of the order Spodosols, Xerumbrepts (Brown Podzolic soils), and Vitrandepts (Regosols) *(63)*.

Soils within the range of Rocky Mountain Douglas-fir originated also from a considerable array of parent materials. In south-central British Columbia, eastern Washington, and northern Idaho, soils vary from basaltic talus to deep loess with volcanic ash to thin residual soil over granitic or sedimentary rocks. They are mostly Vitrandepts and Xerochrepts. Parent materials in Montana and Wyoming consist of both igneous and sedimentary rocks, and locally of glacial moraines. Soils derived from noncalcareous substrates are variable in texture but consistently gravelly and acidic. A significant portion of the sedimentary rocks is limestone, which gives rise to neutral or alkaline soils ranging in texture from gravelly loams to gravelly silts. Limestones often weather into soils that are excessively well drained. Soils are Cryoboralfs of the order Alfisols, and Cryandepts and Cryochrepts of the order Inceptisols. Soils in the central and southern Rocky Mountains are very complex. They developed from glacial deposits, crystalline granitic rocks, conglomerates, sandstones, and, in the Southwest, limestones. These soils are Alfisols (Gray Wooded soils), Mollisols (Brown Forest soils), Spodosols (Brown Podzolic soils, Podzols), and Entisols *(2,46)*.

Altitudinal distribution of both varieties of Douglas-fir *(menziesii* and *glauca)* increases from north to south, reflecting the effect of climate on distribution of the species. The principal limiting factors are temperature in the north of the range and moisture in the south. Consequently, Douglas-fir is found mainly on southerly slopes in the northern part of its range, and on northerly exposures in the southern part. At high elevations in the southern Rocky Mountains, however, Douglas-fir grows on the sunny slopes and dry rock exposures *(56)*.

Generally, the variety *glauca* (fig. 3) grows at considerably higher altitudes than the coastal variety of comparable latitude. Altitudinal limit for Douglas-fir in central British Columbia is about 760 m (2,500 ft) but rises to 1250 m (4,100 ft) on Vancouver Island. In Washington and Oregon, the species generally occurs from sea level to 1520 m (5,000 ft), although locally it may occur higher. In the southern Oregon Cascades and in the Sierra Nevada, the altitudinal range is between 610 and 1830 m (2,000 and 6,000 ft). In river valleys and canyon bottoms, the species may occasionally occur at elevations of 240 to 270 m (800 to 900 ft). Near the southern limit of its range in the Sierra Nevada, the species grows to elevations of 2300 m (7,500 ft). The inland variety grows at elevations from 550 to 2440 m (1,800 to 8,000 ft) in the northern part of its range. In the central Rocky Mountains, Douglas-fir grows mostly at elevations between 1830 and 2590 m (6,000 and 8,000 ft), and in the southern Rocky Mountains, between 2440 and 2900 m (8,000 and 9,500 ft). In some localities in southern and central Arizona, Douglas-fir may be found as low as 1550 m (5,100 ft) in canyon bottoms. The highest elevation at which Douglas-fir grows in the Rocky Mountains is 3260 m (10,700 ft) on the crest of Mount Graham in southeastern Arizona.

Associated Forest Cover

Periodic recurrence of catastrophic wildfires created vast, almost pure stands of coastal Douglas-fir throughout its range north of the Umpqua River in Oregon. Although logging has mainly eliminated

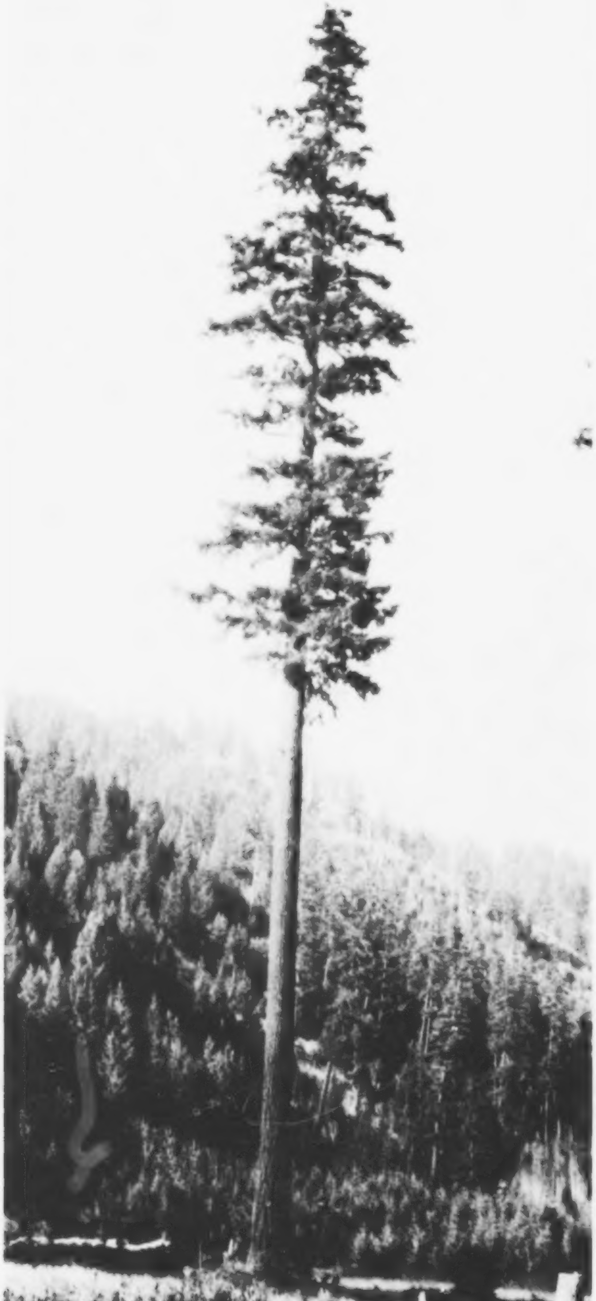

Figure 3—*A good stand of second-growth Rocky Mountain Douglas-fir covering the hillside behind a mature tree.*

the original old-growth forest, clearcutting combined with slash burning has helped maintain Douglas-fir as the major component in second-growth stands. Where regeneration of Douglas-fir was only partially successful or failed, red alder *(Alnus rubra)* has become an associate of Douglas-fir or has replaced it altogether.

Rocky Mountain Douglas-fir grows in extensive pure stands, uneven- and even-aged, in southern Idaho and northern Utah and in western Montana as a broad belt between ponderosa pine and spruce-fir zones. At high elevations or northerly latitudes, more cold-tolerant mountain hemlock *(Tsuga mertensiana)*, whitebark pine *(Pinus albicaulis)*, true firs *(Abies* spp.), Engelmann spruce *(Picea engelmannii)*, western white pine *(Pinus monticola)*, and lodgepole pine *(Pinus contorta)* gradually replace Douglas-fir. Douglas-fir yields to ponderosa pine *(P. ponderosa)*, incense-cedar *(Libocedrus decurrens)*, Oregon white oak *(Quercus garryana)*, California black oak *(Q. kelloggii)*, canyon live oak *(Q. chrysolepis)*, and interior live oak *(Q. wislizeni)* on droughty sites, and to western redcedar *(Thuja plicata)*, maples *(Acer* spp.), red alder, black cottonwood *(Populus trichocarpa)*, and other broad-leaved species on poorly drained sites.

Toward the fog belt of the Pacific coast, Douglas-fir gives way to Sitka spruce *(Picea sitchensis)*, western hemlock *(Tsuga heterophylla)*, and western redcedar. The variety *menziesii* is a major component of four forest cover types *(20)*: Pacific Douglas-Fir (Society of American Foresters Type 229), Douglas-Fir-Western Hemlock (Type 230), Port Orford-Cedar (Type 231), and Pacific Ponderosa Pine–Douglas-Fir (Type 244). It is a minor component of the following types:

221	Red Alder
223	Sitka Spruce
224	Western Hemlock
225	Western Hemlock–Sitka Spruce
226	Coastal True Fir–Hemlock
227	Western Redcedar–Western Hemlock
228	Western Redcedar
232	Redwood
233	Oregon White Oak
234	Douglas-Fir–Tanoak–Pacific Madrone

The variety *glauca* is a principal species in three forest cover types: Interior Douglas-Fir (Type 210), Western Larch (Type 212), and Grand Fir (Type 213). It is a minor species in five types: Engelmann Spruce–Subalpine Fir (Type 206), White Fir (Type 211), Western White Pine (Type 215), Aspen (Type 217), and Lodgepole Pine (Type 218).

Wherever Douglas-fir grows in mixture with other species, the proportion may vary greatly, depending on aspect, elevation, kind of soil, and the past history of an area, especially as it relates to fire. This is particularly true of the mixed conifer stands in the southern Rocky Mountains where Douglas-fir is associated with ponderosa pine, southwestern white pine (*Pinus strobiformis*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), Engelmann spruce, and aspen (*Populus* spp.).

The most important shrubs associated with coastal Douglas-fir *(21)* through its central and northern range are vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Pacific rhododendron (*Rhododendron macrophyllum*), Oregongrape (*Berberis nervosa*), red huckleberry (*Vaccinium parvifolium*), and salmonberry (*Rubus spectabilis*). Toward the drier southern end of its range, common shrub associates are California hazel (*Corylus cornuta* var. *californica*), oceanspray (*Holodiscus discolor*), creeping snowberry (*Symphoricarpos mollis*), western poison-oak (*Toxicodendron diversilobum*), ceanothus (*Ceanothus* spp.), and manzanita (*Arctostaphylos* spp.).

Principal understory species associated with variety *glauca* differ within its range *(3)*. In the northern part, they are common snowberry (*Symphoricarpos albus*), white spirea (*Spirea betulifolia*), ninebark (*Physocarpus malvaceus*), and pachistima (*Pachistima myrsinites*). In the central part, they are true mountain-mahogany (*Cercocarpus montanus*), squaw currant (*Ribes cereum*), chokeberry (*Prunus virginiana*), big sagebrush (*Artemisia tridentata*), western serviceberry (*Amelanchier alnifolia*), and bush rockspirea (*Holodiscus dumosus*); in the southern part they are New Mexico locust (*Robinia neomexicana*), Rocky Mountain maple (*Acer glabrum*), and oceanspray *(3)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Douglas-fir is monoecious; trees commonly begin to produce strobili at 12 to 15 years of age, although observations of younger seedlings bearing ovulate strobili have been reported.

Primordia of both pollen and seed cone buds are present when the vegetative bud breaks in the spring of the year before the cone crop. But neither can be distinguished from primordia of vegetative buds for the first 10 weeks of their existence. By mid-June, histochemical differences separate the pollen cone primordia, which are usually clustered near the base of the extending shoot, from the seed cone primordia, which are borne singly near the acropetal end of the shoot, and from the vegetative bud primordia *(5)*. These three primordia may be microscopically identified in mid-July; by September, the egg-shaped pollen cone buds are easily distinguished by the naked eye from the darker vegetative buds and the larger seed cone buds.

The size of the cone crop is determined by the number of primordia that differentiate and develop into buds, not by the number formed. Poor cone crops, then, reflect a high abortion rate of primordia the preceding year. Large numbers of pollen or seed cone buds in the fall merely indicate the potential for a heavy cone crop the following year. Damaging frost during cone anthesis or depredations by insects may destroy most of the cones and seeds before they mature *(19)*.

Male strobili are about 2 cm (0.8 in) long and range from yellow to deep red. Female strobili are about 3 cm (1.2 in) long and range from deep green to deep red *(45)*. They have large trident bracts and are receptive to pollination soon after emergence.

Anthesis and pollination of variety *menziesii* occur during March and April in the warmer part of the range and as late as May or early June in the colder areas. At low and middle elevations, Douglas-fir cones mature and seeds ripen from mid-August in southern Oregon to mid-September in northern Washington and southern British Columbia. Mature cones are 8 to 10 cm (3 to 4 in) long. The bracts turn brown when seeds are mature *(45)*. Seedfall occurs soon after cone maturity with, generally, two-thirds of the total crop on the ground by the end of October. The remaining seeds fall during winter and spring months. In British Columbia, seedfall starts later and lasts longer—less than half the seeds fall by late October and more than one-third fall after March 1. In general, Douglas-fir seedfall in the fog belt of western North America is more protracted than in the drier areas east of the summit of the Coast Ranges.

The phenology of flowering is similar for variety *glauca*; early flowering occurs in mid-April to early May in Colorado and as late as early May to late June in northern Idaho. Cone ripening varies from late July at the lower elevations (about 850 m or 2,800 ft) in Montana to mid-August in northern Idaho. Seed dispersal of *glauca* begins in mid-August in central Oregon and occurs as late as mid-September at higher elevations (about 1710 m or 5,600 ft) in Montana *(45)*.

Seed quality varies during the seedfall period. It is high in the fall but declines rapidly during winter and spring. This pattern probably reflects the fact that cone scales in the center of the cone, where the highest quality seed are borne, open early and scales at the tip and base of the cone, which bear generally poorly formed seeds, open late.

Both cones and seeds vary greatly in size; the smaller seeds (about 132,000/kg or 60,000/lb) occur on trees in British Columbia and the larger seeds (about 51,000/kg or 23,000/lb), on trees in California. Seeds of variety *glauca* are slightly heavier and more triangular in shape than seeds of *menziesii*. Size is determined before fertilization, so there is no correlation between weight of seed and genetic vigor, although seedlings germinated from heavier seeds may be slightly larger the first few months of growth than those grown from lighter seeds. Because the range in seed size from any one tree is relatively small, however, fractionation of seed lots to segregate the heavier seed may reduce the genetic variation and actually eliminate traits from certain populations.

Douglas-fir seed crops occur at irregular intervals—one heavy and one medium crop every 7 years on the average; however, even during heavy seed years, only about 25 percent of the trees produce an appreciable number of cones *(34)*. Trees 200 to 300 years old produce the greatest number of cones. For example, a stand of old-growth Douglas-fir may produce 20 to 30 times the number of cones per hectare that a second-growth stand 50 to 100 years old produces.

Seed Production and Dissemination—Major deterrents to natural regeneration of Douglas-fir include limited seed supply; consumption of seed by insects, animals, and birds; competing plant species; and unfavorable environments. Although reports of fully stocked stands resulting from seedfall from sources 1 to 2 km (0.6 to 1.2 mi) distant are not rare, the great majority of Douglas-fir seeds fall within 100 m (330 ft) of a seed tree or stand edge *(18)*.

Data describing the quantities of seeds that may fall vary widely, but most years are characterized by less than 2.2 kg/ha (2 lb/acre), of which no more than 40 percent is sound. Years with poor seed crops generally have a lower percentage of viable seeds, perhaps because the low incidence of fruiting trees may favor a higher level of selfing *(25)*.

Seedling Development—Douglas-fir germination is epigeal. Seed germinates in mid-March to early April in the warmer portions of the range and as late as mid-May in the cooler areas. Seedling growth the first year is indeterminate but relatively slow and limited generally by moisture, which triggers initiation of dormancy in midsummer. The dormant period normally extends from midsummer until April or May of the following year *(37)*. Douglas-fir can produce lammas shoots, but this habit is confined to either the more moist portion of the range or to years with abnormally heavy summer rainfall. This habit is probably most pronounced in the southern Rockies, where the summer period is characterized by irregular, heavy rainstorms. In any event, the great majority of the annual shoot growth occurs during the initial flush. First-year seedlings on better sites in the Pacific Northwest may develop shoots 6 to 9 cm (2.5 to 3.5 in) long. Growth in subsequent years is determinate and gradually accelerates so that when saplings are 8 to 10 years old, terminal growth may consistently exceed 1 m (3.3 ft) per year on the more productive sites.

Seedlings of the variety *menziesii* normally survive best when the seed germinates on moist mineral soil, but *menziesii* will tolerate a light litter layer. Seedlings do not survive well, however, on heavy accumulations of organic debris. In contrast, seedlings of the variety *glauca* are favored by a duff layer, especially in the larch forests of northwestern Montana *(53)*.

First-year seedlings survive and grow best under light shade, especially on southerly exposures, but older seedlings require full sunlight. Particularly in the fog belt, competing vegetation such as alder, maple, salmonberry, and thimbleberry *(Rubus parviflorus)* limits Douglas-fir regeneration by creating intolerable levels of shade; plants such as grasses, manzanita, ceanothus, and oak compete strongly for available moisture; and plants such as bracken *(Pteridium aquilinum)* and vetch *(Vicia* spp.) smother small seedlings with leaves and other debris. Successful regeneration of variety *menziesii* often depends on weed control in the commercial range of Douglas-fir because many associated plant species have growth rates much greater than that of juvenile Douglas-fir *(8)*. For this reason, regeneration may be more reliable after a wildfire, which destroys the reservoir of potential competitive species, than after a harvest operation, which leaves areas well suited to the rapid proliferation of the herbaceous and woody competitors of Douglas-fir.

In the Rocky Mountains, competing vegetation may promote the establishment of variety *glauca* seedlings by reducing temperature stress and may inhibit seedling growth by competing strongly for moisture. The latter effect is most pronounced in the southern portions of *glauca*'s range.

Microsites with adverse moisture and temperature conditions frequently limit establishment of both *menziesii* and *glauca* seedlings on southerly aspects *(32)*. Soil surface temperatures in excess of 65° C (149° F) are prevalent in the southern Cascade Range and Siskiyou Mountains and are common in the Cascades even as far north as Mount Rainier. Prolonged droughts, which may extend from May through September, are frequent in southern Oregon and northern California, and low annual precipitation and high evaporation stress greatly limit the distribution of *glauca* in the Rocky Mountains.

Like nearly all perennial woody plants, Douglas-fir is dependent on a mycorrhizal relationship for efficient uptake of mineral nutrients and water. Approximately 2,000 species of fungi have been identified as potential symbionts with Douglas-fir, and both ectomycorrhizal and ectendomycorrhizal structures have been observed on this species *(59)*. Occasionally, nursery practices result in seedlings with few mycorrhizae, but no deficiencies in mycorrhizal infection have been reported for natural seedlings.

Historically, large burned or cleared areas in the range of variety *menziesii*, such as those on Vancouver Island *(52)*, have naturally seeded into nearly pure stands of Douglas-fir. On mesic to moist sites this process may occur over a relatively short period, perhaps 10 to 15 years. On drier sites, such regeneration may be quite protracted and require a hundred or more years. Stocking of harvested areas has been extremely variable during the past 30 years, and large tracts in the drier or cooler portions of the range are covered by brush species such as manzanita, ceanothus, salmonberry, salal, or lower value hardwoods, such as alder, maple, and oak.

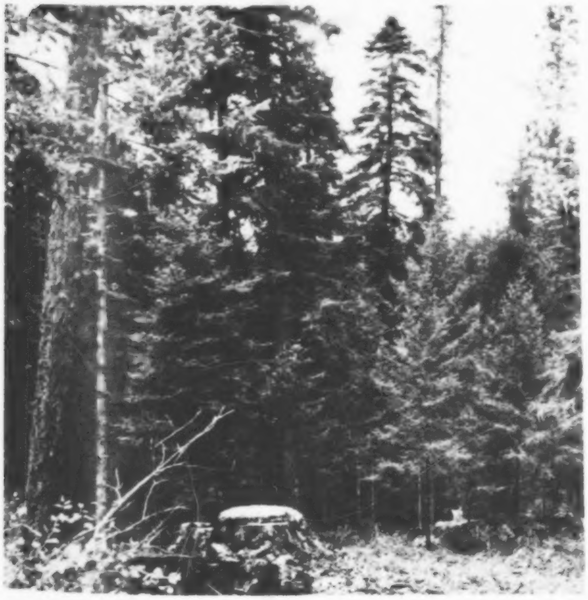

Figure 4—*Thrifty young trees and good reproduction in a cutover Douglas-fir forest in New Mexico.*

Regeneration of variety *glauca* in the Rocky Mountains (fig. 4) has also been variable. In general, *glauca* may be considered a seral species in moist habitats and a climax component in the warmer, drier areas. Regeneration is favored where Douglas-fir is seral, especially in northern Idaho and western Montana where a strong maritime influence modifies the generally continental climate that prevails in the central and southerly Rocky Mountains. In contrast, regeneration of Douglas-fir is poor where the species has attained climax status *(49)*.

From 1950 until about 1970, large areas of cutover and burned-over forest land in the Pacific Northwest were aerially seeded. Direct seeding suffers from the same deficiencies as natural regeneration, however; that is, stands produced are often uneven in stocking and require interplanting or precommercial thinning, and animals destroy a large proportion of the seeds. With the advent of greatly increased forest nursery capacity, direct seeding is much less common *(13,54)*.

Vegetative Reproduction—Douglas-fir does not naturally reproduce vegetatively. Substantial research to develop cuttings as a regeneration procedure has demonstrated that reliable rooting of cuttings is limited to material collected from trees less than 10 years old, or from trees that have been subjected to repeated shearing to regenerate material with a juvenile habit. A second major impediment to the use of cuttings as a regeneration technique for this species is that most such material has a period of plagiotropic growth, which may be lengthy, before the erect habit is assumed.

Research with tissue culture techniques has demonstrated substantial promise, but widespread use of this technique in reforestation of the Douglas-fir region is, at best, a future possibility.

Sapling and Pole Stages to Maturity

Growth and Yield—Natural stands of coastal Douglas-fir normally start with more than 2,500 trees per hectare (1,000/acre). Planted stands generally have between 750 and 1,500/ha (300 and 600/acre) at the beginning *(9)*. Annual height increment is relatively slow the first 5 years but then begins to accelerate. Coastal Douglas-fir attains the largest height increments between 20 and 30 years of age but retains the ability to maintain a fairly rapid rate of height growth over a long period. Douglas-fir in high-elevation forests of the Oregon-Washington Cascade Range can continue height growth at a substantial rate for more than 200 years

(15). Height growth of Douglas-fir on dry sites at mid-site indices in the Cascade Range of western Oregon is similar to that of upper-slope Douglas-fir in the Washington and Oregon Cascade Range. At higher site indices, however, height growth on dry sites is initially faster but slower later in life; at lower site indices, it is initially slower but faster later in life *(40)*.

On a medium site (III) at low elevations, height growth, which averages 61 cm (24 in) annually at age 30, continues at a rate of 15 cm (6 in) per year at age 100, and 9 cm (3.6 in) at age 120 *(18,39)*. Trees 150 to 180 cm (60 to 72 in) in diameter and 76 m (250 ft) in height are common in old-growth forests *(22)*. The tallest tree on record, found near Little Rock, WA, was 100.5 m (330 ft) tall and had a diameter of 182 cm (71.6 in). Coastal Douglas-fir is very long lived; ages in excess of 500 years are not uncommon and some have exceeded 1,000 years. The oldest Douglas-fir of which there is an authentic record stood about 48 km (30 mi) east of Mount Vernon, WA. It was slightly more than 1,400 years old when cut *(39)*.

Information about yields of coastal Douglas-fir under intensive management for an entire rotation is still limited. It is therefore necessary to rely either on estimates based on yields from unmanaged stands, or on yields from intensively managed stands in regions where Douglas-fir has been introduced as an exotic *(12)*, or on growth models *(16)*. If measured in cubic volume of wood produced, range in productivity between the best and poorest sites is more than 250 percent. Depending on site quality, mean annual net increments at age 50 vary from 3.7 to 13.4 m^3/ha (53 to 191 ft^3/acre) in unmanaged stands *(39)*. Estimates of gross yields may increase these values as much as 80 percent, depending on mensurational techniques and assumptions. Comparisons of gross yields from unmanaged stands with those from managed stands of the same site indexes in Europe and New Zealand suggest that yields in managed stands will be considerably higher than would be indicated by estimates based on yields in unmanaged stands. Presumably, managed stands of coastal Douglas-fir can produce mean annual increments of 7 m^3/ha (100 ft^3/acre) on poor sites and exceed 28 m^3/ha (400 ft^3/acre) on the highest sites under rotations between 50 and 80 years *(55)*. Although information on productivity of Douglas-fir in terms of total biomass production is still limited, indications are that it may reach 1000 t/ha (447 tons/acre) on high sites *(22)*.

The interior variety of Douglas-fir does not attain the growth rates, dimensions, or age of the coastal variety. Site class for Rocky Mountain Douglas-fir is usually IV or V (site index 24 to 37 m or 80 to 120 ft at age 100) when compared with the growth of this species in the Pacific Northwest *(1,43)*. On low sites, growth is sometimes so slow that trees do not reach saw-log size before old age and decadence overtake them. Interior Douglas-fir reaches an average height of 30 to 37 m (100 to 120 ft) with a d.b.h. between 38 and 102 cm (15 and 40 in) in 200 to 300 years. On the best sites, dominant trees may attain a height of 49 m (160 ft) and a d.b.h. of 152 cm (60 in) *(23)*. Diameter growth becomes extremely slow and height growth practically ceases after age 200. Interior Douglas-fir, however, appears capable of response to release by accelerated diameter growth at any size or age *(35)*. The interior variety is not as long lived as the coastal variety and rarely lives more than 400 years, although more than 700 annual rings have been counted on stumps *(23)*.

Gross volume yields for Douglas-fir east of the Cascades in Oregon and Washington range from 311 m^3/ha (4,442 ft^3/acre) for site index 15.2 m or 50 ft (at age 50) to 1523 m^3/ha (21,759 ft^3/acre) for site index 33.5 m (110 ft) *(14)*. In the northern Rocky Mountains, estimates of yield capabilities of habitat types where Douglas-fir is climax range from about 1.4 to 7 m^3/ha (20 to 100 ft^3/acre) per year to more than 9.8 m^3/ha (140 ft^3/acre) per year in some of the more moist habitat types where Douglas-fir is seral *(46)*.

Information on yields of Douglas-fir in the southern Rocky Mountain region is scant. In New Mexico, a virgin stand of Douglas-fir (61 percent) and associated species averaged 182 m^3/ha (13,000 fbm/acre). Occasionally, stands yield as high as 840 m^3/ha (60,000 fbm/acre). Annual growth rates from 2.0 to 3.9 m^3/ha (140 to 280 fbm/acre) after partial cutting have been reported in New Mexico *(17)*.

Rooting Habit—Although Douglas-fir is potentially a deep-rooting species, its root morphology varies according to the nature of the soil. In the absence of obstructions, Douglas-fir initially forms a tap root that grows rapidly during the first few years. In deep soils (69 to 135 cm, 27 to 53 in), it was found that tap roots grew to about 50 percent of their final depth in 3 to 5 years, and to 90 percent in 6 to 8 years; however, boulders or bedrock close to the soil surface result in quick proliferation of the original tap root. Platelike root systems develop when Douglas-fir grows in shallow soils or soils with a high water table. Main lateral branches develop during the first or second growing season as branches of the tap root. These structural roots tend to grow obliquely into deeper soil layers and contribute to anchoring a tree. The majority of roots in the surface soil are long ropelike laterals of secondary and tertiary origin. Fine roots, those less than 0.5 cm (0.2 in) in diameter, develop mostly from smaller lateral roots and are concentrated in the upper 20 cm (8 in) of soil *(29)*. Fine roots have a short lifespan, ranging in general from a few days to several weeks. Cyclic death and replacement of fine roots changes seasonally, reflecting changes in environmental conditions *(51)*.

Size of the root system appears to be related to size of the crown rather than the bole. In British Columbia, ratios of root spread to crown width averaged 1.1 for open- and 0.9 for forest-grown Douglas-fir, but greater lateral spread has been observed on poorly drained sand and sandy gravel soils. The radial symmetry of root systems seems to be readily distorted by slope, proximity to other trees, and presence of old roots. Observations in the Pacific Northwest and the Rocky Mountains indicate that roots of Douglas-fir extend farther downslope than upslope.

The proportion of root biomass decreases with age and may vary from 50 percent at age 21 to less than 20 percent in stands older than 100 years *(29)*. Root grafting is very common in stands of Douglas-fir, often leading to a system of interconnected roots in older stands *(36)*.

Reaction to Competition—Except in its youth, when it is reasonably tolerant of shade, coastal Douglas-fir is classed as intermediate in overall shade tolerance, below most of its common associates in tolerance to shade *(42)*. Of these associates, ponderosa pine, Jeffrey pine *(Pinus jeffreyi)*, incense-cedar, noble fir *(Abies procera)*, and red alder are more demanding of light. In its interior range, Douglas-fir ranks intermediate in tolerance among its associates, being more tolerant than western larch, ponderosa pine, lodgepole pine, southwestern white pine, and aspen *(23)*.

The coastal variety is a seral species, except on extremely dry sites in southwestern Oregon and northern California. In its interior range, Douglas-fir is both a climax and a seral species. In the northern Rocky Mountains, it replaces ponderosa pine, lodgepole pine, and western larch above the ponderosa pine belt, and in turn is replaced by western redcedar, western hemlock, Engelmann spruce, grand fir, and subalpine fir on cooler and wetter sites. In the southern Rocky Mountains, Douglas-fir is a climax species in several habitat types of mixed conifer forest and a seral species in the spruce–fir forests *(4)*.

The natural occurrence of Douglas-fir in extensive stands is mainly a consequence of forest fires. The species' rapid growth and longevity, the thick corky bark of its lower boles and main roots, combined with its capacity to form adventitious roots, are the main adaptations that have enabled Douglas-fir to survive less fire-resistant associates and to remain a dominant element in western forests. Without fire or other drastic disturbance, Douglas-fir would gradually be replaced throughout much of its range by the more tolerant hemlock, cedar, and true fir. Old-growth forests of Douglas-fir tend to show wide ranges in age structure—rather than being even-aged—which indicates that Douglas-fir was not established over short periods after major fires or other disturbances *(22)*.

Stands of vigorous Douglas-fir can be successfully regenerated by any of the even-aged methods. Clearcutting in combination with planting is the most widely used method. In stands infected with dwarf mistletoe *(Arceuthobium* spp.), clearcutting is the best alternative for eliminating the disease. If clearcutting on good sites results in establishment of red alder, Douglas-fir is at a severe disadvantage. Alder has very rapid juvenile growth on high sites and can easily over top and suppress Douglas-fir. If Douglas-fir is released in time, however, its subsequent development will actually benefit from the nitrogen fixed by red alder. Nitrogen is the only nutrient in forest soils of the Pacific Northwest *(41)* and Intermountain Northwest *(44)* that has been shown to be limiting to growth of Douglas-fir.

Because of its ability to tolerate shade in the seedling stage, the shelterwood system is a feasible alternative to clearcutting in coastal stands *(64)*. Shelterwood cutting has been practiced only on a limited scale in the Pacific Northwest, however, where the large dimensions of old-growth timber, danger of blowdown to the residual stand, and probability of brush encroachment limit its use. In the Rocky Mountains, shelterwood cutting has been more commonly applied and with good results *(50)*. Where interior Douglas-fir is climax, the true selection method can be used. It is unsuitable for coastal Douglas-fir.

Although Douglas-fir may be regenerated either naturally or artificially from seed, the erratic spacing characteristic of many naturally regenerated stands and the general lack of reliability of this system have resulted in legislation (Forestry Practices Acts) in Washington, Oregon, and California that virtually mandates artificial regeneration. And, because direct seeding also produces variable results, the regeneration system uses 2-year-old bare root seedlings, 3-year-old transplants, year-old container-grown seedlings, or 2-year-old transplants that were grown the first year in containers *(9)*. Such planting stock may be affected by agents discussed here under the heading "Damaging Agents" or may suffer mortality from a lack of vigor occasioned by improper production and harvest practices, from poor planting practices, and from frost damage incurred either in nursery beds or after planting *(13)*.

When Douglas-fir develops in a closed stand, the lower limbs die rapidly as they are increasingly subjected to overhead shade. Nevertheless, natural pruning is exceedingly slow because even small dead limbs resist decay and persist for a very long period. On the average, Douglas-fir is not clear to a height of 5 m (17 ft) until 77 years old, and to 10 m (33 ft) until 107 years. Obviously, natural pruning will not produce clear butt logs in rotations of less than 150 years. Artificial pruning will greatly reduce the time required to produce clear lumber but may result in severe grain distortion and brittle grain structure around pruning wounds *(10)*.

Seedlings and saplings of Douglas-fir respond satisfactorily to release from competing brush or overstory trees if they have not been suppressed too severely or too long. Trees of pole and small sawtimber size in general respond very well to thinning. Trees that have developed in a closed stand, however, are poorly adapted to radical release, such as that occasioned by very heavy thinning. When exposed, the long slender boles with short crowns are highly susceptible to damage from snowbreak, windfall, and sunscald. Sudden and drastic release of young Douglas-fir may cause a sharp temporary reduction in height growth *(57)*. Application of a nitrogen fertilizer in combination with thinning gives better growth responses in Douglas-fir than either fertilizer or thinning alone *(41)*.

Damaging Agents—From seed to maturity, Douglas-fir is subject to serious damage from a variety of agents. Douglas-fir is host to hundreds of fungi, but relatively few of these cause serious problems. Various species of *Pythium, Rhizoctonia, Phytophthora, Fusarium,* and *Botrytis* may cause significant losses of seedlings in nurseries *(58,60)*, whereas *Rhizina undulata*, shoestring root rot *(Armillaria mellea)*, and laminated root rot *(Phellinus weirii)* have caused significant damage in plantations. In fact, the latter two fungi represent a serious threat to management of young-growth stands of Douglas-fir, especially west of the summit of the Cascades. Trees die or are so weakened that they are blown over. Effective control measures are not available. Of the many heart rot fungi (more than 300) attacking Douglas-fir, the most damaging and widespread is red ring rot *(Phellinus pini)*. Knots and scars resulting from fire, lightning, and falling trees are the main courts of infection. Losses from this heart rot far exceed those from any other decay. Other important heart rot fungi in the Pacific Northwest are *Fomitopsis officinalis, F. cajanderi,* and *Phaeolus schweinitzii (28)*. In the Southwest, *Echinodontium tinctorium, Fomitopsis cajanderi,* and *F. pinicola* are important.

Several needle diseases occur on Douglas-fir. The most conspicuous, a needlecast, is caused by *Rhabdocline pseudotsugae*. It is mainly a disease of younger trees, reaching damaging proportions only after prolonged periods of rain while the new needles are appearing. The interior variety is particularly susceptible to the disease but is less often exposed to long periods of rain during the spring growth period.

The most damaging stem disease of Douglas-fir is *Arceuthobium douglasii*. This dwarf mistletoe occurs throughout most of the range of Douglas-fir *(26)*.

Over 60 species of insects are indigenous to Douglas-fir cones, but only a few species damage a significant proportion of the seed crop. Damage by insects is frequently more pronounced during the years of light or medium seed crops that may follow good or heavy crops.

The most destructive insects include: (a) the Douglas-fir seed chalcid *(Megastigmus spermotrophus)*, which matures in the developing seed and gives no external sign of its presence; (b) the Douglas-fir cone moth *(Barbara colfaxiana)* and the fir cone worm *(Dioryctria abietivorella)* whose larvae bore indiscriminately through the developing cones and may leave external particles of frass; and (c) the Douglas-fir cone gall midge *(Contarinia oregonensis)* and cone scale midge *(C. washingtonensis)*, which destroy some seed but prevent harvest of many more by causing galls that prevent normal opening of cones. The Douglas-fir cone moth is perhaps a more serious pest in the drier, interior portions of the Douglas-fir range and the *Contarinia* spp. in the wetter regions. Any of these insects, however, may effectively destroy a cone crop in a given location *(27)*.

Insects are generally not a severe problem for Douglas-fir regeneration, although both the strawberry root weevil *(Otiorhynchus oratus)* and cranberry girdler *(Chrysoteuchia topiaria)* may cause significant damage to seedlings in nurseries; damage to plantations by rain beetles *(Pleocoma* spp.) and weevils *(Steremnius carinatus)*—the latter particularly damaging to container-grown-plants—has been reported.

The Douglas-fir tussock moth *(Orgyia pseudotsugata)* and the western spruce budworm *(Choristoneura fumiferana)* are the most important insect enemies of Douglas-fir. Both insects attack trees of all ages at periodic intervals throughout the range of interior Douglas-fir, often resulting in severe defoliation of stands. The Douglas-fir beetle *(Dendroctonus pseudotsugae)* is a destructive insect pest in old-growth stands of coastal and interior Douglas-fir. Its impact is diminishing, however, with the change to second-growth management and rotations of less than 100 years *(24)*.

Consumption of Douglas-fir seeds by small forest mammals such as white-footed deer mice, creeping voles, chipmunks, and shrews, and birds such as juncos, varied thrush, blue and ruffed grouse, and song sparrows further reduces seed quantity. A single deer mouse may devour 350 Douglas-fir seeds in a single night. Mouse populations of 7 to 12/ha (3 to 5/acre) are not uncommon. Most seedfall occurs at least 150 days before the germination period, so this single rodent species has the capacity to destroy the great majority of natural seedfall. Spot seeding studies in the Western United States have clearly demonstrated that forest mammals destroy virtually all unprotected seed.

Browsing and clipping by hares, brush rabbits, mountain beaver, pocket gophers, deer, and elk often injure seedlings and saplings. Recent reports have indicated that such damage in western Oregon and Washington may strongly affect seedling survival in many plantations *(7,61)*. In drier areas, domestic livestock have caused considerable damage to variety *glauca* plantations by grazing and trampling seedlings. In pole-sized timber, bears sometimes deform and even kill young trees by stripping off the bark and cambium.

High winds following heavy rains occasionally cause heavy losses from blowdown in the Pacific Northwest. Heavy snow and ice storms periodically break the tops of scattered trees in dense young stands. Crown fires, when they occur, destroy stands of all ages. The thick bark of older Douglas-firs, however, makes them fairly resistant to ground fires.

Special Uses

Douglas-fir is grown as a Christmas tree on rotations ranging from 4 to 7 years. Trees are sheared each year to obtain a pyramid-shaped crown. Attempts to grow Douglas-fir as a Christmas tree in North America outside its native range have failed. Coastal Douglas-fir is usually killed by frost, and the interior variety suffers too much from the needle cast disease *Phaeocryptopus gaeumanni*.

Genetics

The genus *Pseudotsuga* includes two species *(P. menziesii* and *P. macrocarpa)* indigenous to North America and five species native to Asia. All except *P. menziesii* have a karyotype of 2N=24, the number of chromosomes characteristic of Pinaceae. But the Douglas-fir karyotype is 2N=26, a probable reason for the general failure of hybridization trials with this species *(56)*.

Population Differences

Pseudotsuga menziesii has two widely recognized varieties: *menziesii*, the green variety indigenous to the area west of the summit of the Cascade Range in Washington and Oregon and of the Sierra Nevada in California; and *glauca*, the blue Douglas-fir native to the interior mountains of the Pacific Northwest and the Rocky Mountains in the United States, and to Mexico. The division between the two varieties is not as clearly defined in Canada, although *menziesii* is commonly considered indigenous to the area west of the crest of the mainland Coast and Cascade Ranges.

The varieties differ in both growth rate and size at maturity, *menziesii* being more rapid growing and much larger. In habit, *glauca* is more shade tolerant, has a more pronounced tap root, is more susceptible to *Rhabdocline pseudotsugae* when grown in a moist environment, and is significantly more cold hardy. The coastal and interior varieties also differ in botanical and morphological characteristics. Because of variation within the two recognized varieties, it has been suggested that variety *glauca* be replaced with several varieties, and many forms have been reported. Chemical and cytological investigations have shown differences both between and within the two varieties, but such work has not led to further differentiation *(38,48)*.

Races

Douglas-fir has one of the broadest ranges of any North American conifer, much of it over extremely dissected terrain, and the species exhibits a great deal of genetic differentiation. Much of this variation is strongly associated with geographic and topographic features *(47)*. Thus, clinal patterns of variation in growth and phenological traits have been observed over north–south, east–west, and elevational transects despite the appreciable gene flow expected in this species. Adaptive patterns of genetic variation also occur among Douglas-fir populations within local regions. For example, evidence exists for "aspect races" in variety *menziesii*: Seedlings grown from seed collected on the more xeric southern aspects grow slower, set buds earlier, and form larger roots in relation to shoots than seedlings grown from seeds collected on adjacent north-facing slopes. Seedlings from seed sources on the south aspect have characteristics consistent with adaptation to the shorter growing seasons and drier soil conditions generally found on south-facing slopes and may be better able to survive under drought stress than seedlings from north-aspect seed sources *(33)*. Topoclinal variation in response to microenvironmental heterogeneity has also been found in the central part of the Oregon Cascades *(11)*.

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Sequoia sempervirens (D. Don) Endl. **Redwood**

Taxodiaceae **Redwood family**

David F. Olson, Jr., Douglass F. Roy, and Gerald A. Walters

Redwood *(Sequoia sempervirens)*, also called coast redwood and California redwood, is native to the central and northern California coast, a region of moderate to heavy winter rain and summer fog so vital to this tree. It is one of three important North American trees of the family Taxodiaceae. Close relatives are the giant sequoia *(Sequoiadendron giganteum)* of the Sierra Nevada in California and the baldcypress *(Taxodium distichum)* of the southeastern states.

Habitat

Native Range

The range of redwood (fig. 1) extends southward from two groves on the Chetco River in the extreme southwest corner of Oregon (lat. 42° 09′ N.), to Salmon Creek Canyon in the Santa Lucia Mountains of southern Monterey County, CA (lat. 35° 41′ N.). This redwood belt is an irregular coastal strip about 724 km (450 mi) long and generally 8 to 56 km (5 to 35 mi) wide *(39)*. Within this region, redwood trees grow now, or could grow, on an estimated 647 500 ha (1.6 million acres). Of this area, 260 200 ha (643,000 acres) comprise the commercial coast redwood forest type (more than 50 percent redwood stocking). The remainder of the area contains parks, other forest types containing redwood, and recently logged redwood type *(12)*. The old-growth redwood, much of which is in State and National Parks, occupies less than 80 940 ha (200,000 acres) *(36)*. The old-growth in commercial forests will be harvested within the next few decades. A major discontinuity splits the type in southern Humboldt County, CA. South of Sonoma County, CA, redwoods grow in detached and irregular areas to the southern extremity of the range *(38,39)*.

Climate

The mild climate of the redwood forest region can be classed broadly as super-humid or humid. Mean annual temperatures vary between 10° and 16° C (50° and 60° F). Differences between mean annual maximum and mean annual minimum temperatures

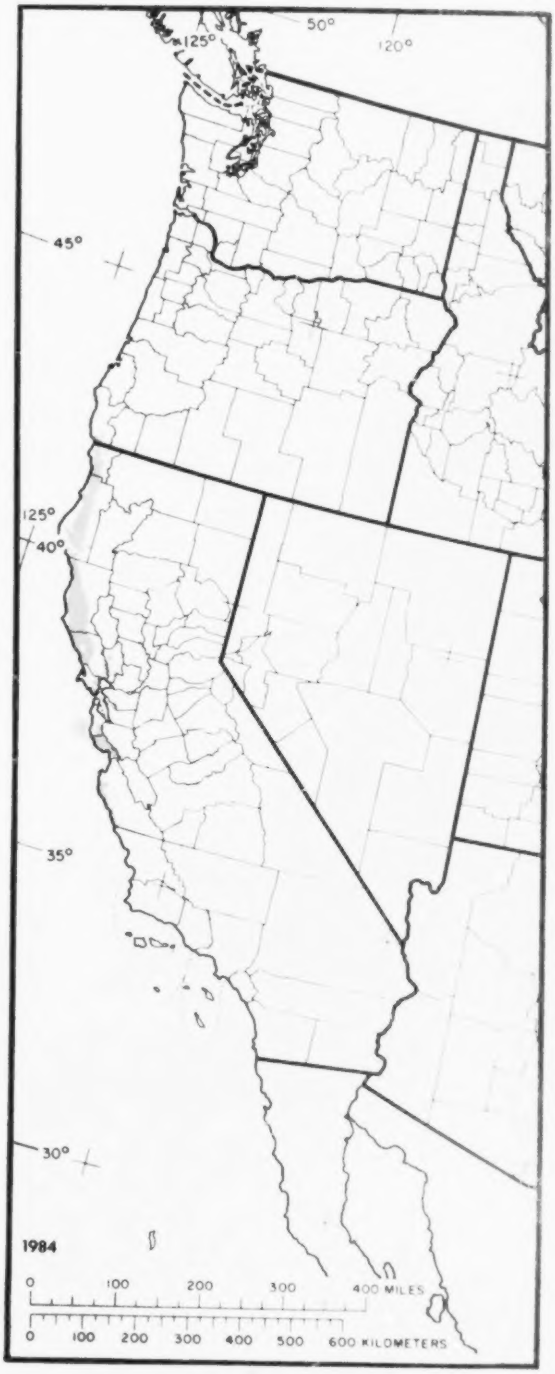

Figure 1—*The native range of redwood.*

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vary from –12° C (10° F) for coastal points to –1° C (30° F) for the eastern edge of the redwood type. Temperatures rarely drop below –9° C (15° F) or rise above 38° C (100° F). The frost-free period varies from 6 to 11 months *(34)*.

Annual precipitation varies between 640 and 3100 mm (25 and 122 in) and is mostly winter rain, although snow sometimes covers the highest ridges. Generally, January is the wettest month and July is the driest. With substantial precipitation in all months except summer, only slight summer drought on deep soils, and mild winters, the climate is productive, and some of the world's grandest forests are indigenous to it *(34)*.

The frequent summer fogs that blanket the redwood region seem to be more significant than the amount of precipitation in delineating the redwood type. The major effect of fog is to decrease water loss from evaporation and transpiration. An additional effect of condensation and fog drip from tree crowns is an increased soil moisture supply during the dry summers *(1)*. The natural range of redwood is limited to areas where heavy summer fogs from the ocean provide a humid atmosphere, although its successful growth in plantations or amenity plantings is not as limited. Redwood is among the most successful trees in the Central Valley of California, and at low elevations in the Sierra Nevada. It grows well at considerable distance from the ocean in New Zealand, France, Spain, and elsewhere *(26,27)*.

Soils and Topography

The parent rock material of the redwood region is largely massive marine sandstone formed in the Tertiary and Upper Mesozoic periods. Considerable shale and lesser amounts of Mesozoic limestones and Franciscan slates, cherts, limestones, and sandstones also are present, and schists are fairly common in some localities.

High-site soils for redwood consist of Xerochrepts, Haploxerults, and Haplohumults of the Hugo, Josephine, Melbourne, Empire, Sites, and Larabee series (orders Inceptisols and Ultisols) and associated alluvial soils. The high-site residual soils have been derived from either consolidated or soft sedimentary rocks. In the Coastal Forest Practice Act District of California, which encompasses the natural range of redwood, the Hugo soil series predominates. In current soil taxonomic terms, the Hugo series is a Typic Distrochrept of the order Inceptisols *(45,46)*. It is a member of a loamy-skeletal, mixed, mesic family, typically pale brown, moderately acid, gravelly (sandy) clay loam A horizons, and pale brown, strongly acid gravelly (sandy) clay loam B horizons. Limits of redwood forests sometimes are determined by soil types. For example, redwood does not grow on soils having high amounts of magnesium and sodium.

Fertility of soils under redwood stands has been studied by measuring the replaceable calcium concentration, expressed in equivalents, present in a square meter (10.76 ft^2) to a depth of 30 cm (12 in). This measure indicates fertility best because it separates nutritional properties from other environmental effects. Equivalents ranged from 4 to more than 80, with 63 appearing to be optimum *(49)*.

Soil nutrient levels that were observed to change during harvest of old-growth or second-growth redwood recovered to nearly original values during regrowth. In the one-meter soil profile, carbon, nitrogen, phosphorus, and exchangeable potassium and sodium increased in amount, while calcium decreased *(52)*. Soil organic matter showed a small decline and recovery after logging *(18)*.

The lowest amount of soil moisture available during the year has been related to minimum basal area growth of redwood stands. Basal area is used as an index of stand development. This minimum available soil moisture, expressed as a percentage of storage capacity, ranged between 18 and 86, with 62 correlated with maximum basal area *(49)*.

The redwood region, generally, is characterized by irregular ridges oriented northwest to southeast with deep narrow valleys. Consequently, the principal streams drain to the northwest. Much of the terrain is rough, steep, and extremely dissected both by major streams and smaller drainages. Redwoods grow from sea level to about 915 m (3,000 ft) elevation, but most are found between 30 and 760 m (100 and 2,500 ft). The best stands have developed on flats and benches along the larger streams, on moist coastal plains, river deltas, moderate westerly slopes, and valleys opening toward the sea.

Although most redwood stands are close to the ocean, redwood does not tolerate ocean winds, and considerable evidence suggests that it is sensitive to ocean salts carried inland during storms. Usually redwoods do not grow on hillsides that face the ocean. The absence of redwood near the ocean also may be caused by the absence of forest soils of sufficient depth and fertility to support redwood.

Redwoods are smaller and give way to other species as altitude, dryness, and slope increase. In the north, redwoods clothe all exposures and reach their maximum development as forest trees. In the southern part of the range, redwoods are restricted to western or northern exposures, and at the extreme southern extension they are restricted almost entirely to the bottoms of narrow canyons that cut through steep foothills abutting the ocean. Trees near the mouths of these canyons often are exposed to onshore winds and frequently have flat tops with dead limbs on the windward side. This effect has been attributed to the trees' inability to replace moisture lost through desiccation by winds.

On alluvial flats, where redwoods reach their maximum development, soils have been built up by deposits of sediment from successive floods. In one area the ground level has been raised 3.4 m (11 ft) in 700 years. In another, repeated flooding in the past 1,000 years deposited nearly 9.1 m (30 ft) of silt and gravel around the bases of many large redwood trees. Deposits from a single flood have been as deep as 76 cm (30 in). Redwoods adapt to the new ground levels by originating new and higher root systems *(43,51)*. This flooding generally kills competing species and thereby allows redwood to maintain nearly pure stands on such plains.

Associated Forest Cover

Redwood is a principal species in only one forest cover type, Redwood (Society of American Foresters Type 232) *(42)*, but is found in three other Pacific Coast types, Pacific Douglas-Fir (Type 229), Port-Orford-Cedar (Type 231), and Douglas-Fir–Tanoak–Pacific Madrone (Type 234).

Pure stands of redwood are found only on some of the best sites, usually the moist river flats and gentle slopes below 305 m (1,000 ft). Although redwood is a dominant tree throughout its range, generally it is mixed with other conifers and broad-leaf trees.

Douglas-fir *(Pseudotsuga menziesii)* is well distributed throughout most of the redwood type. Distributions of other conifer associates are more limited. Significant species on the coastal side of the redwood type are grand fir *(Abies grandis)* and western hemlock *(Tsuga heterophylla)* north from northern Sonoma County, CA, and Sitka spruce *(Picea sitchensis)* north from the vicinity of Humboldt Bay, CA.

Conifers associated less commonly on the coastal side of the redwood type are Port-Orford-cedar *(Chamaecyparis lawsoniana)*, Pacific yew *(Taxus brevifolia)*, western redcedar *(Thuja plicata)*, and California torreya *(Torreya californica)*. Other conifers found with redwood include Gowen cypress *(Cupressus goveniana)* and several species of pine, including bishop pine *(Pinus muricata)*, knobcone pine *(P. attenuata)*, lodgepole pine *(P. contorta)*, Monterey pine *(P. radiata)*, and sugar pine *(P. lambertiana)*.

The two hardwoods most abundant and generally distributed in the redwood region are tanoak *(Lithocarpus densiflorus)* and Pacific madrone *(Arbutus menziesii)*. Other hardwoods found with redwood include vine maple *(Acer circinatum)*, bigleaf maple *(A. macrophyllum)*, red alder *(Alnus rubra)*, giant chinkapin *(Castanopsis chrysophylla)*, Oregon ash *(Fraxinus latifolia)*, Pacific bayberry *(Myrica californica)*, Oregon white oak *(Quercus garryana)*, cascara buckthorn *(Rhamnus purshiana)*, willows *(Salix* spp.), and California-laurel *(Umbellularia californica)*.

Of the great variety of lesser vegetation found in association with redwood, these species are especially common: bracken *(Pteridium aquilinum* var. *lanuginosum)*, sword fern *(Polystichum munitum)*, salal *(Gaultheria shallon)*, blueblossom *(Ceanothus thyrsiflorus)*, California huckleberry *(Vaccinium ovatum)*, Pacific rhododendron *(Rhododendron macrophyllum)*, salmonberry *(Rubus spectabilis)*, coyotebrush *(Baccharis pilularis)*, and snowbrush *(Ceanothus velutinus)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Redwood is monoecious; inconspicuous male and female flowers are borne separately on different branches of the same tree. The ovulate conelets grow into broadly oblong cones *(10)*. Redwood female strobili become receptive and pollen sheds between late November and early March, although flowering usually is over by the end of January. Weather conditions during pollination may directly affect seed quality. Continuous rains during flowering wash pollen from the male strobili and little pollen may reach the receptive female strobili. Dry periods during pollination permit better pollen dispersal and improve seed viability.

Redwood cones are terminal and are 13 to 29 mm (0.5 to 1.1 in) long. They mature in autumn of the first year after flowering and are open from early September until late December. Although cones persist for several months, they open and shed seeds soon after ripening.

Seed Production and Dissemination—Redwoods start to bear seeds when 5 to 15 years old *(8)*. One study showed that seed viability increased with the age of parent trees *(38,39)*. Maximum seed viability was reached when trees were more than 250 years old. Seeds produced by trees younger than 20 years generally were less than 1 percent viable, and seeds from trees more than 1,200 years old were not more than 3 percent viable. Redwoods produce abundant seeds almost every year. Even trees in the intermediate crown class often produce seed crops. Fair to abundant crops were produced in 5 consecutive years in north coastal California *(8)*. Cones often are rare, however, or nonexistent on large areas for many years in stands in Mendocino County, CA (central part of the range). Large mature stands on Maui, HI, have few or no cones or pollen *(27)*.

Trees with new, narrow crowns resulting from sprouting of dormant buds after fire has killed the crown produce few cones during the first 4 years after the fire. About one-half such narrow-crowned trees, locally called fire-columns, bear cones in the fifth year, and almost all produce cones by the seventh or eighth year.

The germination rate of redwood seeds is usually low. Poor germination often results from a low percentage of sound seeds (less than 15 percent) rather than from dormancy. When obviously defective seeds are removed, germination rarely is below 80 percent, and is sometimes 100 percent *(27)*. Identification of defective seeds often is difficult, however, because many seeds appearing sound are filled with tannin. In one seed study, soundness varied significantly with seed size. Seeds passing 12, 10, and 8 mesh screens were 2, 8, and 15 percent sound, respectively. Seeds from seven populations were photographed by X-ray. The distribution in categories was as follows: seeds empty or tannin filled, 58 to 97 percent; seeds from embryos damaged by fungi, 0 to 11 percent; and sound seeds, 1 to 32 percent *(38,39)*.

Although only scant evidence is recorded on storage of redwood seeds, they do not seem to store well. One seed lot was stored successfully for 3 years but lost its viability completely after 5 years *(19)*.

Redwood cones dry readily under conditions of low humidity and quickly release their seeds with slight shaking. But because weather conditions at cone ripening in nature usually are unfavorable for rapid drying, seed dispersal may be spread over periods that vary considerably in length. Rains, however, may hasten seed dissemination. One observer found in many instances that redwood seeds remained in the open cones until a drenching rain dissolved the tannic crystals in the cones *(38,39)*. Seed dissemination during the winter months seems characteristic of redwood in the northern stands. More than four-fifths of the sound seeds in one study were shed during December and January.

Redwood seeds are small and light, number about 265,000/kg (120,000/lb), but lack efficient wings to slow them in falling *(10)*. They fall at rates between 1.5 and 6.2 m/s (4.9 and 20.5 ft/s), averaging 2.6 m/s (8.6 ft/s). These rates are faster than for most other wind-disseminated forest seeds and limit seed dispersal considerably.

Timbered edges of clearcut units have effective seeding distances of only 61 m (200 ft) uphill and 122 m (400 ft) downhill under average redwood stand conditions. A recent study in Del Norte County, CA, showed that the largest clearcut units should not be more than 12 to 16 ha (30 to 40 acres) if regeneration will be completed by natural seeding *(38,39)*. No silvicultural reasons exist for restricting the size of clearcuts, if areas are regenerated by artificial methods. Maximum size of clearcuttings is specified in Forest Practice Rules, based on erosion hazard, or other criteria.

Seedling Development—Redwood seeds, generally, are ready to germinate soon after they fall to the ground if seedbeds are moist and the weather is warm enough. Redwood seeds do not require pretreatment to germinate, but germination speed is increased by an overnight soak in aerated water *(27)*. Mineral soil is the best seedbed, but seeds will germinate readily in duff, on logs, in debris, or under other vegetation, and in either shade or full sunlight if adequate soil moisture is available. Redwood seed germination is epigeal.

New redwood seedlings require a greater supply of soil moisture for survival than that needed by seedlings of most associated trees *(19)*. Late spring and early fall rains can be critical survival factors. Apparently, redwoods have no root hairs. Consequently, redwood roots do not seem to function efficiently in extracting soil moisture. This fact may limit natural distribution to sites where favorable water relations result from high rainfall, humid air, moist soil, or low summer temperatures, or from various combinations of these conditions. Redwood seedlings on fully exposed soil can withstand considerable surface heat if their roots have reached a permanent moisture supply. Otherwise, they die before soil surface temperatures reach 60° C (140° F). Redwood seedlings are extremely vulnerable to infection by damping-off and *Botrytis* fungi during their first year *(22)*.

In its early stages, redwood grows rapidly in height. Seedlings often grow about 46 cm (18 in) in the first season and trees 4 to 10 years old sometimes grow 0.6 to 2.0 m (2 to 6.5 ft) in a year. In many instances, however, rapid height growth of trees that originate from seed does not commence until the trees are more than 10 years old.

Juvenile growth of redwood is best in full sunlight. Although redwood seedlings can endure heavy shade, growth there is slow. Photosynthetic capacity in redwood is remarkably high at low light intensities and keeps increasing as light intensity increases, much like more intolerant species. Redwood grew vigorously in much weaker light than 12 other tree species studied *(38,39)*. For example, it increased its size 8.8 times in 10 percent of full sunlight in a 9-month period, more than twice the growth of any of the other species in the test. For appreciable growth, Engelmann spruce *(Picea engelmannii)* and Douglas-fir require twice as much light as redwood. Pine requires three to four times as much.

Radial growth of redwood in Mendocino County, CA, at points 6, 14, and 32 km (4, 9, and 20 mi) from the coast did not vary markedly in growth pattern. Radial growth began after mid-March, increased to a maximum in late May, and then declined at a fairly uniform rate to a minimum at the end of September. Radial growth was negligible from October 1 to March 15.

Vegetative Reproduction—Redwood can be propagated by cuttings, but few large-scale attempts of this kind have been reported. In an early study in California, 40 percent of the cuttings from the tops of fast-growing seedlings that had been pushed into forest nursery soil with no special treatment developed root systems *(38,39)*. Currently, rooting in excess of 90 percent is obtained routinely, with mist in a favorable medium, using juvenile cuttings from seedlings *(27)*. Cuttings from older trees are more difficult to root.

Studies in the past 10 years have improved the cutting procedure by hedging—a technique that seems to maintain the juvenility of the donor tree. A single seedling and its clonal descendants can produce about 1 million cuttings in 3 years by repeated hedging of seedlings and their descendants *(29)*.

Modern methods of plant tissue culture also have propagated redwood successfully *(3)*. Tissues from outstanding mature trees may be cultured in nutrient medium, becoming undifferentiated masses of cells or callus. In different nutrient media, fragments of the callus can be induced to differentiate into small plants. When these plants become large enough, juvenile cuttings can be taken from them *(30)*. In France, scientists have found that shoots of redwood 10 to 20 mm (0.4 to 0.8 in) long are the best reactive material for producing explants, with fragments of the annual shoots being more reactive than the annual sprouts of 2-year-old shoots *(13)*. Tissue cultured plantlets are generally twice the size of seedlings of the same age *(2)*.

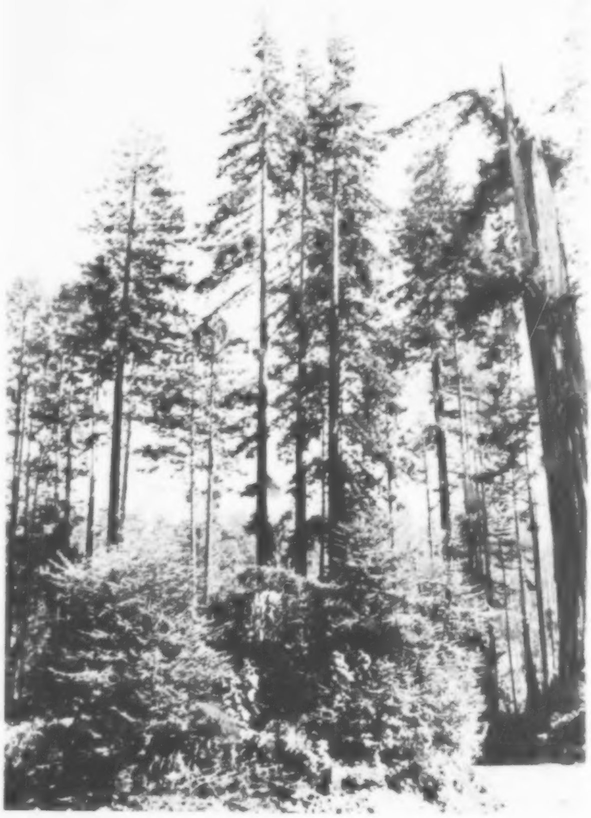

Figure 2—*Redwood sprouting in an area cut 2 or 3 years earlier. New sprouts around a stump are shown in foreground; center background is filled with a cluster of young trees from sprouts.*

Redwood can sprout from stumps and root crowns anytime of the year (fig. 2). Numerous and vigorous sprouts originate from both dormant and adventitious buds within 2 to 3 weeks after logging. Sprouting capacity is related to variables associated with tree size or age. Stumps of small young trees sprout more readily than those of large old trees *(35)*. Stumps often are circled by more than 100 sprouts. Many sprouts may be necessary to sustain a healthy stump-root system *(4,15)*. Powers and Wiant *(37)* found that sprout vigor was related to sprout density. Sprout vigor was reduced at densities less than one sprout per 2 feet of stump circumference. Each sprout soon develops its own root system, and in a remarkably short time the dominant sprouts create circles of new trees around the old stumps.

Depending on the intensity of thinning or partial cutting in redwood, sprouts grow and develop successfully in openings *(11,31)*. A recent study showed that more than 90 percent of all redwood stumps sprouted in a 40-year-old redwood stand thinned to 25, 50, and 75 percent of the initial basal area. Consequently, all thinned stands contained several

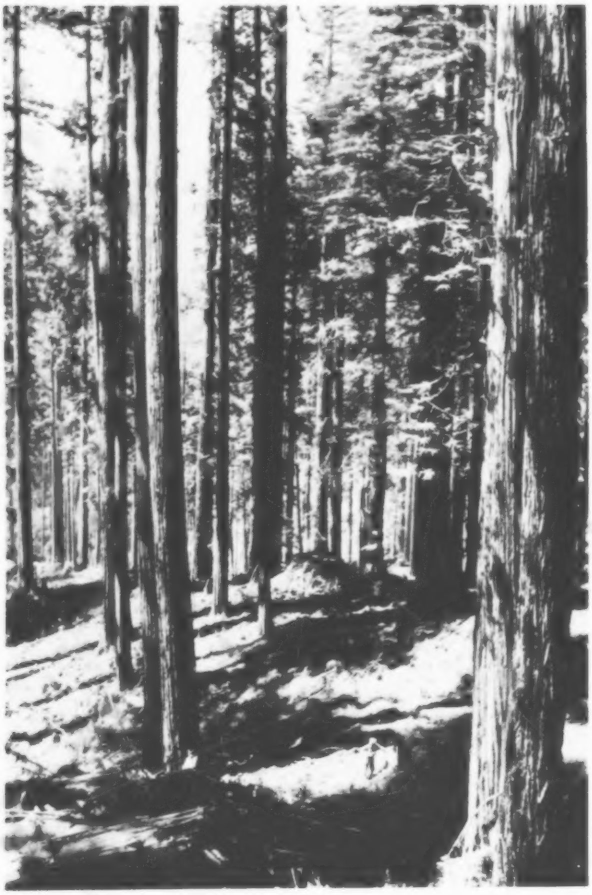

Figure 3—*Redwoods in an experimental forest.*

hundred redwood sprout clumps per acre, and several thousand individual sprouts. The heavier the thinning, the more sprouts developed into vigorous young crop trees *(31)*.

Sprouting by redwood is principally from root crowns, but sprouts sometimes grow from the sides and tops of stumps. These high sprouts are less desirable because they are mechanically weak and not as vigorous as root-crown sprouts. Sprouts originating from the sides and top of stumps often are destroyed by strong wind.

Sprouts are commonly about 60 to 90 cm (24 to 36 in) tall at the end of the first year but may be more than 1.8 m (6 ft) tall. In one instance, a fire killed all sprouts around a stump. About 300 new sprouts appeared within a few days, and at the end of one growing season many reached 2.1 m (7 ft). Sprouts grow more rapidly than seedlings and the initial impetus lasts many years. However, the best phenotypes at age 40 to 80 in stands originating from both sprouts and seedlings often are found to be of seedling origin *(27)*.

Early estimates of stocking from root crown sprouts varied from 20 to 35 percent of full stocking. A later study showed that redwood sprouts on old growth cutover redwood land in Mendocino and Humboldt Counties, CA, provided only 8 percent of full stocking. This finding is low compared to more recent stand examinations where the majority of redwood stems in 163 moderately to fully stocked young growth stands originated from sprouts *(33)*.

Redwood can also sprout along almost the entire length of its trunk. If the crown of a tree is destroyed by fire or mechanically damaged, or the stem is suddenly exposed to light, numerous dormant buds along the trunk are stimulated and produce new foliage. Most of the trunk is then covered by feathery foliage extending 0.6 to 0.9 m (2 to 3 ft) from the trunk. Eventually, normal crowns develop again.

Sapling and Pole Stages to Maturity

Growth and Yield—Redwood (fig. 3) is long lived, grows taller than any other tree species in the world, and is exceeded in bulk only by the giant sequoia. Redwoods are sexually mature at 10 years or less but continue to increase in volume for centuries. The oldest redwood found so far, determined by growth ring counts, is nearly 2,200 years old. Old-growth redwood forests sometimes are incorrectly called even-aged and overmature when, in fact, few forests in the world can match many redwood stands in range of ages and mixture of vigorously growing and decadent trees.

Redwood probably is best known for its great size, although the average redwood is smaller than commonly believed. Trees larger than 30 cm (12 in) in d.b.h. on a 12-ha (30-acre) old-growth tract in Humboldt County, CA, fell approximately into these divisions: 30 to 77 cm (12 to 30 in) in d.b.h., 50 percent; 78 to 153 cm (31 to 60 in), 32 percent; 155 cm (61 in) and larger, 18 percent. Redwoods 366 to 488 cm (144 to 192 in) in d.b.h., found scattered over the entire range, are considered large. Trees 610 cm (240 in) or more in diameter at a point 1.5 m (5 ft) above the ground are rare.

Redwoods more than 61 m (200 ft) tall are common, and many trees growing on riverside benches, where soils are deep and moist, are taller than 91 m (300 ft). The tallest measured redwood was 112.1 m (367.8 ft) in 1964 *(50)*.

Large trees and dense stocking combine to produce high yields. More than 81 percent of the commercial

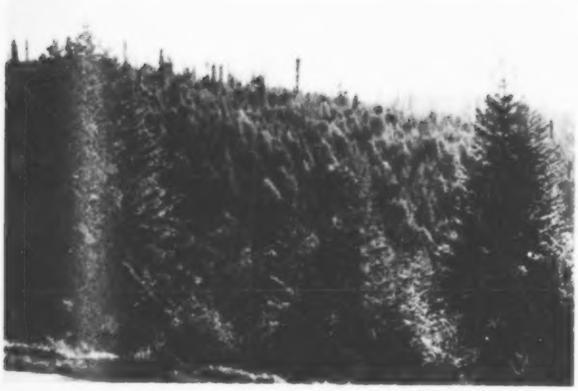

Figure 4—*A young redwood stand with some Douglas-fir on an area from which almost all trees and snags have been removed.*

redwood forest land is classified as highly productive, and only 2 percent is poor for growing trees. Flats along rivers have yielded approximately 10 500 to 14 000 m^3/ha (about 750,000 to 1,000,000 fbm/acre) in scaled logs. Harvest cuttings in Del Norte County, CA, on units of 5.3 ha (13 acres) and larger, produced gross volumes ranging from 1330 to 3921 m^3/ha (95,000 to 280,000 fbm/acre, Scribner).

Biomass accumulates to record levels. A redwood stand in Humboldt State Park in California provides the greatest biomass ever recorded, with a stem biomass of 3461 t/ha (1,544 tons/acre) *(20)*.

Economical conversion of old-growth redwood to young managed stands by shelterwood or selection cutting is difficult because net growth is negative during the decade after logging. Windthrow, slow growth of residual trees, and damage to established reproduction when residual trees are removed contribute to economic losses. Considering effect on growth, small clearcuttings seem to be a good method for converting old-growth redwood to young managed stands *(9)* (fig. 4).

Young-growth redwood is often nearly as spectacular in size and yield as old growth. Dominant young-growth trees on good sites are 30.5 to 45.7 m (100 to 150 ft) tall at 50 years, and 50.3 to 67.1 m (165 to 220 ft) at 100 years. Height growth is most rapid up to the 35th year. On the best sites, however, height growth continues to be rapid well past 100 years *(24,33)*.

Diameter growth of individual young trees can be rapid or extremely slow. In dense stands where competition is severe, annual diameter increment is commonly less than 1 mm (0.03 in). Occasionally, 40 or more rings per centimeter (more than 100/in) can be counted. At the other extreme, diameter growth sometimes exceeds 2.5 cm (1 in) a year. One redwood growing with little competition was 213 cm (84 in) in d.b.h. when 108 years old.

The yield of young-growth redwood stands at 100 years is expected to range from 742 m^3/ha (10,600 ft^3/acre) on low sites to 3576 m^3/ha (51,080 ft^3/acre) on high sites *(32)*. The same stands yield 781 to 4998 m^3/ha (55,760 to 357,000 fbm/acre International quarter-inch rule), and yields of more than 2800 m^3/ha (about 200,000 fbm/acre International quarter-inch rule) are common in young-growth redwood stands. At earlier ages, however, the greatest yields are in stands that contain a mixture of redwood and Douglas-fir *(25)*.

Natural pruning in young redwood stands often is not good. Although live crowns may be limited to the upper third of the trunk, dead limbs are persistent. Branch stubs, although decayed, may remain more than 50 years. In old trees, some branch stubs have affected the quality of the timber over a 200-year period. Trees in the intermediate crown class, however, often prune well naturally, and some trees in a heavily stocked stand have clean trunks for 23 to 30 m (75 to 100 ft) at 85 years.

Rooting Habit—Redwoods have no taproots, but lateral roots are large and wide-spreading. Small trees have better-than-average windfirmness, and large redwoods are windfirm under most conditions.

A study in extreme northwestern California indicated that a combination of wet soil and strong winds is necessary for significant windfall damage. Consequently, windfall is caused by only a few of the many winter storms. Storms that cause windfall come mainly from the south. Uprooting accounted for 80 percent of the redwood windfall in this study *(7)*.

Reaction to Competition—The redwood forest is a climax type. When growing with other species, redwood usually is a dominant tree. Douglas-fir can keep pace with redwood on many sites and occupy dominant and codominant crown positions along with redwood. Redwood has been classed as tolerant or very tolerant, the two highest categories in a scale of five shade tolerance classes. It is probably most accurately classed as very tolerant of shade in most situations.

Redwood stands are dense. At 60 years, redwood may have a basal area of more than 126 m^2/ha (550 ft^2/acre) on the best sites *(32)*. Heavy stocking is desirable because the relatively high tolerance permits land to support a large number of dominant and codominant trees per unit area.

Under some conditions, redwood can endure suppression almost indefinitely. A 25-cm (10-in) suppressed tree might be more than 100 years old. Small trees may be suppressed for more than 400 years but still maintain a remarkable capacity to accelerate growth rates when released if they have not been crowded too closely and are not injured seriously during logging or slash burning. Large trees also can accelerate growth when released from competition.

Damaging Agents—Fire is the principal damaging agent in both young-growth and old-growth stands. The above-ground portions of young stands may be killed outright by a single ground fire, but the stands sprout and reoccupy the site. Fires are especially damaging to trees less than 20 years old because their thin bark does not protect them. Also, more flammable litter lies on the ground, and the microclimate is drier than under old-growth forest.

Old-growth redwood stands show evidence of three or more severe fires each century *(23,44)*. In many instances, fires may only reduce the thickness of the protective bark, which may be more than 30 cm (12 in) thick. In other instances, fires cause basal wounds through which heart rots enter. The combination of recurring fires and advancing decay produces large basal cavities called "goose pens." In extreme instances, mature trees may be so weakened mechanically that they fall.

In its northern range, in and around Redwood National Park, CA, fire has a moderate ecological role in redwood stands. Light ground fires that do not open the canopy favor western hemlock regeneration but usually eliminate older hemlock from the stand. Douglas-fir establishment is infrequent and unsuccessful under a full overstory canopy, even following light ground fires on mesic sites. Relatively hot fires appear essential for the establishment of Douglas-fir trees in discrete age classes. Redwood, grand fir, and tanoak maintain their status in redwood stands with and without the influence of fire *(47,48)*.

Frequency distributions of fires indicate a natural pattern of several short intervals between fires followed by one or more long interval. This suggests that prescribed burning to maintain ecosystems should also be done on a short-short-long interval pattern *(23)*.

Redwood has no tree-killing diseases other than seedling diseases previously listed, but heart rots cause extensive cull. Most common heart rot in the southern part of the range of redwood is a brown cubical rot, caused by *Poria sequoiae*. Most significant farther north is a white ring rot caused by *P. albipellucida (5,22)*.

A twig branch canker *(Coryneum* spp.) has been observed on sprouts and plantation trees of seedling and sapling size. This canker, which girdles stems and branches, could become damaging in plantations *(5,22)*.

Several insects are found on redwood but none cause significant damage. These include a flatheaded twig borer and girdler *(Anthaxia aeneogaster)*, two redwood bark beetles *(Phloeosinus sequoiae* and *P. cristatus)*, and the sequoia pitch moth *(Vespamima sequoiae) (21)*.

Bark stripping by the American black bear has caused serious damage in some parts of the redwood region. Wide strips of bark are ripped from the tree, often from the top to the ground, during April to August. Trees 10 to 30 years old and 15 to 25 cm (6 to 10 in) in diameter are damaged most and many may be girdled. Woodrats often injure planted trees on cutover land and occasionally attack sprouts and larger trees.

In a few instances, redwood is deformed by fasciation, a flattening of the normally cylindrical stem by formation of a row of linked meristems. The causes of most fasciations are unknown *(40)*.

Special Uses

Redwood is used where decay resistance is important. Clark and Scheffer *(14)* found that decay resistance varied among trees or within the heartwood of individual trees. Decay resistance decreased from outer to inner hardwood. Wood classified as very decay resistant was about five times more prevalent in old-growth than in young-growth trees.

A prominent special feature of the redwood is its production of burls from which beautifully figured table tops, veneers, bowls, and other turned products are cut. These burls are found on any part of the trunk and in sizes varying from an inch to many feet in diameter. Their cause is unknown. Small burls containing hundreds of dormant buds often are cut and placed in shallow containers, kept moist, and allowed to sprout. These live burls serve as attractive house plants.

Another feature of redwood is its extremely tough and fibrous bark. The bark must be removed before logs reach the head saws so that sawing uniform lumber will be possible. The bark is used as hog fuel, insulation, or garden mulch.

Genetics

Sequoia is unique within Coniferales, being of a hexaploid nature *(41)*. It was thought that redwood originated as an allopolyploid from hybrids between early Tertiary or Mesozoic species of *Metasequoia* and some extinct Taxodiaceous plant such as the modern giant sequoia. However, the types and numbers of marker chromosomes found in *Metasequoia* and *Taxodium distichum* are different than those present in *Sequoia*, making it unlikely that these species contributed to the polyploidy of *Sequoia*. Comparisons between the marker chromosomes in *Sequoia* and those in *Sequoiadendron* indicate that genomic contribution by *Sequoiadendron* to *Sequoia* is not probable *(41)*.

Races of redwood are not known, but the following cultivars (cultivated varieties) have been recognized *(16)*:

cv.	'Adpressa'	Tips of shoots creamy white. Awl-like leaves.
cv.	'Glauca'	Leaves 6 mm (0.25 in.) long, glaucous, bluish.
cv.	'Nana Pendula'	Leaves glaucous, branches pendulous.
cv.	'Pendula'	Branches pendulous.
cv.	'Prostrata'	Prostrate at first; leaves green, glaucous beneath.

Four varieties of redwood now available in nurseries show a range of growth habits, texture, color, and form. They are named Aptos Blue, Los Altos, Soquel, and Santa Cruz *(6)*.

An uncommon form of redwood, the albino redwood, has been described in a few locations within the redwood region *(17)*. These albinos result from a genetic disorder and exist by attachment to a normal green tree, generally at the roots. The tallest albino observed was 19.8 m (65 ft) tall. Albinism is often a useful trait in genetics research to determine mutation rate, and for other purposes.

Preliminary results from studies of self and related outcross families indicate that, compared with outcrosses, selfing produced no additional cone abortion or variable effects on germination. Under stress conditions in nurseries and outplantings, some inbreeding depression becomes evident, and restricting inbreeding in redwood seed-orchards seems prudent *(30)*.

The tissue culture techniques described earlier also allow genetic manipulation of redwood at the cellular level. Possibilities being explored include the production of dihaploid redwood from female gametophyte cultures *(2)*.

Hybrids

In Russia, hybridization of redwood with giant sequoia, bald cypress, and Japanese cryptomeria *(Cryptomeria japonica)* has been reported *(38,39)*.

Other attempts to develop a hybrid between coast redwood and giant sequoia by normal controlled-pollination crosses have failed *(28)*. Cell fusion in culture may be used to create interspecific hybrids with giant sequoia or other species *(28)*.

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Sequoiadendron giganteum (Lindl.) Buchholz **Giant Sequoia**

Taxodiaceae **Redwood family**

C. Phillip Weatherspoon

Since its discovery in the mid-nineteenth century, giant sequoia *(Sequoiadendron giganteum)*, also called sequoia, bigtree, and Sierra redwood, has been noted for its enormous size and age, and its rugged, awe-inspiring beauty. Because the species has broad public appeal and a restricted natural range, most groves of giant sequoia have been accorded protected status. Outside its natural range, both in the United States and in many other countries, giant sequoia is highly regarded as an ornamental and shows promise as a major timber-producing species.

Habitat

Native Range

The natural range of giant sequoia (fig. 1) is restricted to about 75 groves scattered over a 420-km (260-mi) belt, nowhere more than about 24 km (15 mi) wide, extending along the west slope of the Sierra Nevada in central California *(16)*. The northern two-thirds of the range, from the American River in Placer County southward to the Kings River, takes in only eight widely disjunct groves. The remaining groves, including all the large ones, are concentrated between the Kings River and the Deer Creek Grove in southern Tulare County *(33)*. Varying in size from less than 1 to 1619 ha (1 to 4,000 acres), the groves occupy a total area of 14 410 ha (35,607 acres) *(17)*.

Climate

Giant sequoia is found in a humid climate characterized by dry summers. Mean annual precipitation in the groves varies from about 900 to 1400 mm (35 to 55 in), with high year-to-year variation. Less than 30 mm (1.2 in) usually falls between June 1 and September 30. Most of the precipitation comes in the form of snow between October and April. Mean annual snowfall ranges from 366 to 500 cm (144 to 197 in), and snow depths of 2.0 m (6.6 ft) or greater are common in midwinter *(32)*.

Mean daily maximum temperatures for July for typical groves are 24° to 29° C (75° to 84° F). Mean minimum temperatures for January vary from 1° to -6° C (34° to 21° F). Extremes are about -24° and 40° C (-12° and 104° F) *(32,37)*.

Low temperatures seem to be a limiting factor for giant sequoia at the upper elevational limits of its range, as well as in areas with severe winters where the species has been introduced. Distribution of the species at low elevations is limited mainly by deficient soil moisture during the growing season *(34)*.

Soils and Topography

Soils are derived from a variety of rock types. Most groves are on granitic-based residual and alluvial soils, and three are on glacial outwash from granite. Schistose, dioritic, and andesitic rocks also are common parent materials *(16,36)*.

Typical soil series are Dome, Shaver, Holland, and Chaix. Characteristic soil families are coarse-loamy, mixed, mesic Dystric Xerochrepts; coarse-loamy, mixed, mesic Entic (and Typic) Xerumbrepts of the order Inceptisols; and fine-loamy, mixed, mesic Ultic Haploxeralfs of the order Alfisols. The natural range of the species lies mostly within the mesic temperature regime, extending only a short distance into the frigid regime, and wholly within the xeric moisture regime *(22)*.

Giant sequoia grows best in deep, well-drained sandy loams. Its density also is much greater in the more mesic sites, such as drainage bottoms and meadow edges, than in other habitats within a grove. Total acreage of these productive sites is small, however. Relatively shallow and rocky soils support vigorous individuals, some large, wherever the trees can become established and where underground water is available to maintain them *(16,32)*.

Soil pH ranges mostly from 5.5 to 7.5, with an average of about 6.5 *(22)*. Long-term site occupancy by giant sequoia appears to develop a soil of high fertility, good base status, and low bulk density *(40)*.

Adequate soil moisture throughout the dry growing season is critical for successful establishment of giant sequoia regeneration, although seedlings do not survive in wet soils *(36)*. One study has shown more available soil moisture within a grove, possibly associated with subterranean flow from higher elevations, than in adjacent forested areas *(34)*. Except for its moisture content, soil apparently plays only a minor role in influencing the distribution of the species, as evidenced by the considerable variability in parent material among groves and the fact that giant sequoia grows vigorously when planted in diverse soils around the world *(16)*.

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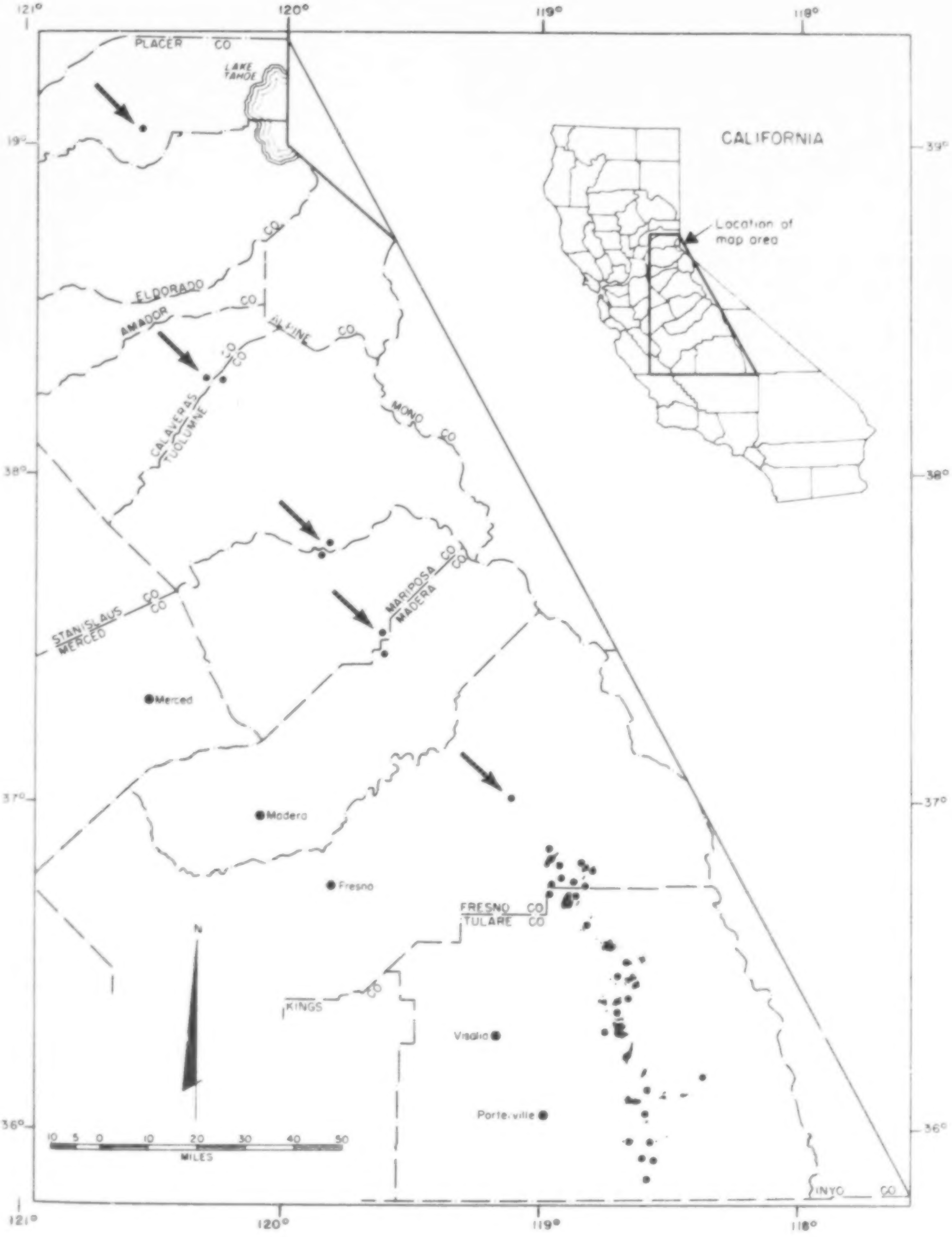
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MONO CO
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MERCED CO
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Merced
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Figure 1—*The native range of giant sequoia.*

Elevations of the groves generally range from 1400 to 2000 m (4,590 to 6,560 ft) in the north, and 1700 to 2150 m (5,580 to 7,050 ft) in the south. The lowest natural occurrence of the species is 830 m (2,720 ft) and the highest is 2700 m (8,860 ft). The eight northern groves are all on slopes of a generally southern aspect. Between the Kings River and the southern boundary of Sequoia National Park, groves appear on north and south slopes with about equal frequency. Farther south, aspects are predominantly northerly *(32)*.

Associated Forest Cover

Giant sequoia groves lie wholly within the Sierra Nevada Mixed Conifer type—SAF (Society of American Foresters) forest cover type 243 *(8)*. A grove is distinguished from similar mesic habitats in this type only by the presence of giant sequoia itself: no other species is restricted to the groves *(33)*. Nowhere does giant sequoia grow in a pure stand, although in a few small areas it approaches this condition *(16)*.

Based on density or canopy coverage, groves typically are dominated strongly by California white fir *(Abies concolor* var. *lowiana)*, despite the presence of emergent individuals of giant sequoia that overtop the canopy. Sugar pine *(Pinus lambertiana)* is a characteristic associate. Incense-cedar *(Libocedrus decurrens)* at low elevations and California red fir *(Abies magnifica)* at high elevations may rival California white fir for dominance. Ponderosa pine *(Pinus ponderosa)* and California black oak *(Quercus kelloggii)* often occupy drier sites within the grove boundaries. Trees less commonly associated with giant sequoia include Jeffrey pine *(Pinus jeffreyi)*, Douglas-fir *(Pseudotsuga menziesii)*, Pacific yew *(Taxus brevifolia)*, Pacific dogwood *(Cornus nuttallii)*, California hazel *(Corylus cornuta* var. *californica)*, white alder *(Alnus rhombifolia)*, Scouler willow *(Salix scoulerana)*, bigleaf maple *(Acer macrophyllum)*, bitter cherry *(Prunus emarginata)*, and canyon live oak *(Quercus chrysolepis)*.

Shrub species most often found in giant sequoia groves are bush chinkapin *(Castanopsis sempervirens)*, mountain misery *(Chamaebatia foliolosa)*, mountain whitethorn *(Ceanothus cordulatus)*, littleleaf ceanothus *(C. parvifolius)*, deerbrush *(C. integerrimus)*, snowbrush *(C. velutinus)*, greenleaf manzanita *(Arctostaphylos patula)*, western azalea *(Rhododendron occidentale)*, *Ribes* spp., *Rosa* spp., and *Rubus* spp. *(16,17,33,36)*.

Stand structure and species frequency vary substantially with elevation, latitude, exposure, soil moisture, and time since fire or other disturbance. In general, protection of groves from fire has resulted in increased prevalence of California white fir, reduced regeneration of giant sequoia and pines, and reduced density of shrubs. The age-class distribution of giant sequoia also varies widely among groves. Most groves today, however, appear to lack sufficient young giant sequoias to maintain the present density of mature trees in the future. In these groves, giant sequoia regeneration evidently has been declining over a period of 100 to 500 years or more *(33)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Giant sequoia is monoecious; male and female cone buds form during late summer. Pollination takes place between the middle of April and the middle of May when the female conelets are only two or three times as large in diameter as the twigs bearing them. Fertilization usually occurs in August, by which time cones are almost full-size. Embryos develop rapidly during the next summer and reach maturity at the end of the second growing season. The egg-shaped mature cones, 5 to 9 cm (2.0 to 3.5 in) in length, yield an average of 200 seeds each *(16,17,36)*.

Seed Production and Dissemination—Cones bearing fertile seeds have been observed on trees as young as 10 years of age, but the large cone crops associated with reproductive maturity usually do not appear before about 150 or 200 years. Unlike most other organisms, giant sequoia seems to continue its reproductive ability unabated into old age. The largest specimens (not necessarily the oldest) bear heavy crops of cones containing viable seeds *(16,36)*.

Giant sequoias have serotinous cones which, at maturity, may remain attached to the stems without opening to release seeds. For 20 years or more, cones may retain viable seeds and continue to photosynthesize and grow, their peduncles producing annual rings that can be used to determine cone age *(16,36)*.

A typical mature giant sequoia produces an average of 1,500 new cones each year, although variability among trees and from year to year is great. Cones produced during years with ample soil moisture are more numerous (more than 20,000 cones on one large tree in an exceptional year) and yield seeds of greater viability than those produced in dry years. The upper third of the crown generally bears at least two-thirds of the cone crop. Because of extended cone retention, a mature tree may have 10,000 to 30,000 cones at any given time, two-thirds of which may be green and closed, and the remainder opened, brown, and largely seedless *(16,17)*.

Estimates of percent germination of seeds removed from green cones range from about 20 to 40 percent *(11,17,38)*. A number of variables, however, account for departures from these average values. Trees growing on rocky sites yield seeds with substantially higher germinability than those on bottom lands with deeper soils. Larger seeds germinate in higher percentages than small ones. In tests of cone age, germination increased from 20 percent for seeds from 2-year-old cones to 52 percent for 5-year-old cones, then dropped to 27 percent for cones 8 years of age. Germinability also varies with cone location in the crown, seed position within the cones, and among groves *(16)*. Artificial stratification of seeds for 60 days or more resulted in faster germination, but not in higher germination percent *(11)*.

Browning or drying of cones, with subsequent shrinkage of scales and dispersal of seeds, is brought about largely by three agents, two of which are animals. The more effective of the two is *Phymatodes nitidus*, a long-horned wood-boring beetle. The larvae of the beetle mine the fleshy cone scales and cone shafts, damaging occasional seeds only incidentally. As vascular connections are severed, scales successively dry and shrink, allowing the seeds to fall. Cones damaged during the summer open several scales at a time, beginning during late summer and fall, and continuing for 6 months to 1 year *(17)*.

The second animal having a significant role in giant sequoia regeneration is the chickaree, or Douglas squirrel *(Tamiasciurus douglasi)*. The fleshy green scales of younger sequoia cones are a major food source for the squirrel. The seeds, too small to have much food value, are dislodged as the scales are eaten. During years of high squirrel densities, the animals tend to cut large numbers of cones and store and eat them at caches. When squirrels are few, most of the cone consumption is in tree crowns—a habit more conducive to effective seed dispersal. The squirrels are active all year *(17)*.

The chickaree prefers cones 2 to 5 years old, whereas *Phymatodes* is more prevalent in cones at least 4 years old. The combined activities of these animals help to ensure that seeds of all age classes are shed, and that rate of seedfall is roughly constant throughout the year and from year to year, despite variability in new cone production. An average rate is about 1 million seeds per hectare (400,000/acre) per year *(17)*.

The third and perhaps most important agent of seed release is fire. Hot air produced by locally intense fire and convected high into the canopy can dry cones, resulting in release of enormous quantities of seed over small areas—for example, 20 million/ha (8 million/acre) *(17)*. This increased seedfall coincides both spatially and temporally with fire-related seedbed conditions favorable for seed germination and seedling survival (fig. 2).

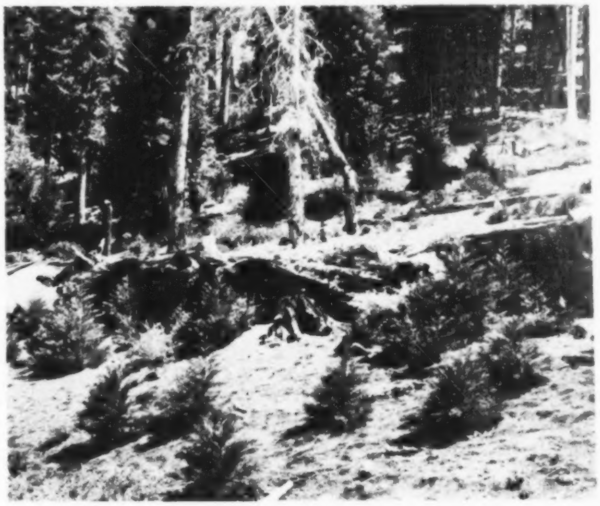

Figure 2—*Young sequoias which came in after a fire burned slash and humus (California).*

Giant sequoia seeds are well adapted for wind dispersal. They are light (average 200,000/kg [91,000/lb]), winged, and fall in still air at a rate of 1.2 to 1.8 m (4 to 6 ft) per second. Winds common in late summer and winter storms in the Sierra Nevada can disperse seeds more than 0.4 km (0.25 mi) from the tall crowns of mature trees *(16,36)*.

Cone and seed insects other than *Phymatodes* have only a minor impact on seed production *(17)*.

Birds and mammals exert a negligible effect on giant sequoia seeds on the ground. Sequoia seeds consistently rank at or near the bottom in food preference tests that include seeds of associated species, primarily because they are small and contain little energy *(17,38)*.

Seedling Development—Natural reproduction in giant sequoia is an unusually tenuous process. Of the enormous numbers of seeds shed each year, extremely few encounter the combination of conditions necessary to become successfully established seedlings.

In contrast with most coniferous seeds, a large majority of seeds of giant sequoia die from desiccation and solar radiation soon after reaching the forest floor, especially during the summer. In one study, viability of seeds removed from fresh cones and placed on the ground dropped from 45 percent to 0 in 20 days. Seeds collected from the forest floor showed an average viability of 1 percent *(17)*.

Seed dormancy is not evident in giant sequoia, so surviving seeds germinate as soon as conditions are favorable *(17)*. Germination is epigeal. The most significant requirement for germination is an adequate supply of moisture and protection of the seed from desiccation. This is best provided by moist, friable mineral soil that covers the seed to a depth of 1 cm (0.4 in), and that is partially shaded to reduce surface drying. A wide range of temperatures is acceptable for germination. The generally sandy soils of the groves normally provide the additional requirement of adequate aeration and the optimum pH range of 6 to 7 *(38)*. Because of rapid percolation, however, adequate moisture retention for germination and initial root development is often marginal.

Seeds dropped just before the first snow or just as the snow melts may have the best chance of germinating and becoming successfully established. Seedlings that produce roots early in the season during favorable soil moisture conditions are more likely to survive the dry summer. The first stage of germination—extension of the radicle—sometimes takes place beneath the snow *(16)*.

Thick litter usually dries too quickly for seeds to germinate, and virtually all seedlings that do get started die before their roots can penetrate to mineral soil *(17,36)*. Only in exceptionally wet years do significant numbers of seedlings become established on undisturbed forest floor. The role of damping-off fungi in the mortality of natural giant sequoia seedlings is not well known, but they are almost certainly a greater problem on thick litter than on mineral soil *(2,25)*. After seedlings are established on more favorable seedbeds, a light covering of litter can moderate soil surface temperatures and retard drying *(37)*.

Seedlings rarely become established in dense grass cover, probably because moisture is depleted in the surface soil early in the season *(36)*.

Soil disturbance and increased availability of light and moisture resulting from past logging in some of the groves have led to establishment of several fine young-growth stands dominated by giant sequoia. Mechanical seedbed preparation is currently a legitimate regeneration option in some groves, although such treatment is inconsistent with management direction in most of the natural range of the species.

Of the various types of natural disturbances that may remove litter and bare mineral soil, fire is undoubtedly the most significant. Locally intense or highly consumptive fires are more effective than light surface fires or physical disturbance in promoting germination and subsequent seedling survival and early growth *(17)*. The resulting short-lived friable soil condition facilitates seed penetration beneath the surface and root penetration following germination. Increased wettability in the surface soil layers resulting from high temperatures appears to improve water penetration and retention in the zones important for seeds and young seedlings. Fire also may kill some understory trees, thereby providing more light to speed the development (especially root penetration) of the shade-intolerant giant sequoia seedlings. Additional benefits include providing a surge of available nutrients, reducing populations of fungi potentially pathogenic to seedlings, and killing seeds and rootstocks of competing vegetation *(17)*.

On the other hand, the dark surface and possibly increased insolation resulting from fire may cause more desiccation and heat killing of giant sequoia seeds and seedlings at the surface. Also, populations of endomycorrhizal fungi may be severely reduced temporarily *(17)*. And low-consumption fires, rather than reducing competing vegetation, may instead greatly stimulate germination and sprouting of shrubs. Partially burned litter, in terms of its suitability for successful seedling establishment, ranks between undisturbed forest floor and areas subjected to hot fires *(38)*.

First-year giant sequoia seedlings established on treated—bulldozed or burned or both—areas were 30 to 150 times more numerous than those on undisturbed forest floor *(17)*. Mortality of first-year seedlings during the 3 summer months on one treated area averaged 39 percent, with an additional 25 percent dying during the next 9 months. Desiccation was the primary cause of mortality in the summer. During a year of increased seasonal precipitation, mortality attributable to desiccation decreased, whereas that caused by insects increased to 25 percent of total mortality. Heat canker, damage by birds and mammals, and fungal attacks were of minor importance.

In the same study, direct mortality of first-year seedlings from insect predation ranged from 3 to 18 percent of all seedlings present. Some of the significant additional insect damage probably caused delayed mortality. Largest seedling losses were in areas recently disturbed, especially by fire, probably because alternative food sources were reduced temporarily. Insects responsible for the damage were early instars of *Pristocauthophilus pacificus*, a camel cricket, and larvae of the geometrids *Sabulodes caberata* and *Pero behrensaria*.

Survival of sequoia seedlings for a 7- to 9-year period was 27 percent on areas subjected to a hot burn as opposed to 3.5 percent on other treated substrates. No seedlings survived in undisturbed areas. In another instance, only 1.4 percent of seedlings established following light surface burning were alive after two summers. Mortality slows substantially after the first 2 or 3 years. At the end of 3 years, surviving seedlings usually have root systems that penetrate the soil to depths that supply adequate moisture through the summer, or to about 36 cm (14 in).

Height growth of giant sequoia seedlings in the groves is relatively slow during the first few years, presumably because of competition for light and moisture from the larger trees. Seedlings 7 to 10 years old had grown at an average rate of about 4 cm (1.6 in) per year. Periodic annual height increment from 10 to 20 years was only 5 cm (2 in). Seedlings grew significantly faster on areas subjected to hot burns than they did elsewhere *(17)*.

In contrast, giant sequoia seedlings in the open grow rapidly and, given an even start, can outgrow any associated tree species (fig. 3). Height growth up to 60 cm (24 in) per year is not uncommon *(9)*.

Up to 2 or 3 years of age, seedlings growing in dense shade (less than 25 percent of full sunlight) survive about as well as others, but grow poorly and develop abnormally *(37)*. At higher light levels, one study found moderate reduction in height growth compared with seedlings in full sunlight *(37)*, whereas another study found no significant effect of reduced light on height growth *(17)*. The adverse effects of shade on older giant sequoias are more conspicuous with respect to both mortality and growth reduction.

Vegetative Reproduction—Giant sequoias up to about 20 years of age may produce stump sprouts subsequent to injury *(19)*. Unlike redwood *(Sequoia sempervirens)*, older trees normally do not sprout from stumps or roots. A recent report *(30)*, however, noted sprouts on two small stumps from suppressed trees about 85 years old. Giant sequoias of all ages may sprout from the bole when old branches are lost by fire or breakage *(17,36)*.

Cuttings from juvenile donors root quickly and in high percentages (up to 94 percent) *(3,10,12)*. Limited success has been achieved in rooting cuttings from older (30- or 40-year-old) trees *(3,10)*. Differences in vegetative regeneration capacities between juvenile and older donors may be reduced if cuttings are taken at the time of budbreak, instead of during the dormant period *(24)*.

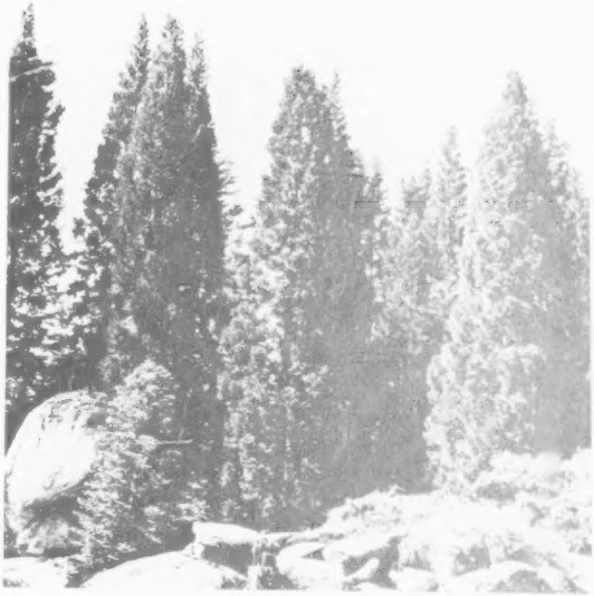

Figure 3—*Young sequoias with characteristic conical crowns (Courtesy National Park Service).*

Sapling and Pole Stages to Maturity

Growth and Yield—One tree species has a greater diameter than giant sequoia, three grow taller, and one lives longer *(16)*. In terms of volume, however, the giant sequoia is undisputedly the world's largest tree (fig. 4). The most massive specimen, the General Sherman tree, located in Sequoia National Park, has an estimated bole volume of 1486 m^3 (52,500 ft^3) *(13)*. The greatest known height for the species is 94.5 m (310 ft), and the greatest mean d.b.h.—for the General Grant tree, in Kings Canyon National Park—is 881 cm (347 in). The indicated mean d.b.h. includes a large abnormal buttress; excluding this abnormality gives a more realistic estimate of the maximum mean d.b.h. for the species—approximately 823 cm (324 in) *(13)*. Mature specimens commonly reach a diameter of 305 to 610 cm (120 to 240 in) above the butt swell and average about 76 m (250 ft) in height *(16)*.

A notable characteristic of mature giant sequoias that contributes substantially to their great volume is the slight taper of the bole—a feature more prominent in this species than in any other Sierra

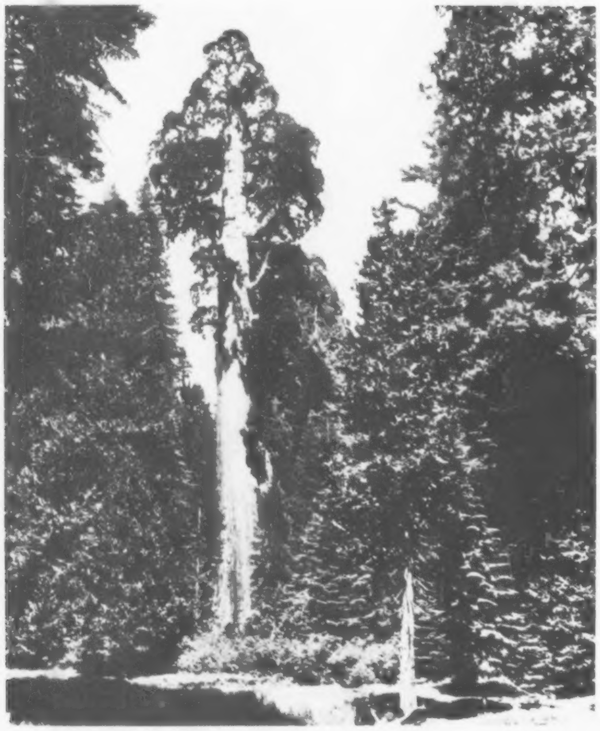

Figure 4—*The General Grant tree (Courtesy National Park Service).*

Nevada conifer *(16)*. In contrast, young open-grown giant sequoias taper markedly.

The greatest known age of a giant sequoia is 3,200 years, determined from a stump count of rings *(16)*. Calculations based on increment borings yield age estimates of 2,000 to 3,000 years for many living trees.

Beyond the seedling stage, giant sequoia unhindered by an overstory continues to grow at least as well as associated species of the same age. In both clearcuts and group selection cuts on a high site in the central Sierra Nevada, it has outgrown other conifers in plantations up to 18 years of age. Furthermore, giant sequoia appears less susceptible than associated conifers to growth reductions caused by shrub competition *(18)*. In a survey of California plantations up to 50 years of age in which giant sequoia had been planted, it outgrew other conifers (mostly ponderosa pine) in most instances in which species differed significantly in height or diameter growth. In the best plantations, giant sequoia averaged 0.5 to 0.7 m (1.6 to 2.3 ft) per year in height growth, and 1.3 to 2.0 cm (0.5 to 0.8 in) in diameter growth per year *(9)*.

Yields of second-growth stands dominated by giant sequoia were found to equal or slightly exceed those of second-growth mixed-conifer stands on the same high sites (site index 53 m [175 ft] at base age 300 years) *(6)*. Volumes at selected stand ages were as follows:

Stand age	**Total volume**	
yr	*m^3/ha*	*fbm/acre (Scribner)*
18	2.6	188
31	83.1	5,938
63	339.3	24,237
86	757.1	54,077

In cubic measure, mean annual increment at age 86 was approximately 9 m^3/ha (126 ft^3/acre).

In contrast to the brittleness and low tensile strength of the wood of old-growth giant sequoia, young-growth trees have wood properties comparable to those of young-growth redwood *(5,28)*. Because most groves have protected status, the potential of the species for fiber production within its natural range is limited. It has been planted widely and often successfully in many parts of the world, however. As in California plantations, on the proper sites it outperforms most other species *(7)*. An 80-year-old giant sequoia plantation in Belgium, for example, grew at an average annual rate of 36 to 49 m^3/ha (514 to 700 ft^3/acre) *(20)*. Many foresters see considerable potential for giant sequoia as a major timber-producing species of the world.

In old-growth groves, rapid height growth continues on the better sites for at least 100 years, producing dense conical crowns. At 400 years, trees range in height from about 34 to 73 m (110 to 240 ft). The rate of height growth declines beyond 400 years, and the typical tree levels off near 76 m (250 ft) at an age of 800 to 1,500 years *(17)*.

Analysis of a large old-growth population showed an average d.b.h. of 48 cm (18.9 in) at 100 years, 132 cm (52.0 in) at 400 years, 219 cm (86.1 in) at 800 years, and 427 cm (168.0 in) at 2,000 years *(17)*.

Although radial growth gradually decreases with age, volume increment generally is sustained into old age. The General Sherman tree, at an approximate age of 2,500 years, has a current radial growth rate at breast height of about 1 mm (0.04 in) per year *(16)*. Average volume increment for this tree since 1931 has been estimated by different methods at 1.13 m^3 (40 ft^3) per year *(16)* and 1.44 m^3 (51 ft^3) per year *(13)*. Therefore, the world's largest tree also may be, in terms of volume increment, the world's fastest-growing tree. A related conclusion can be applied to the species: the enormous size attained by giant sequoia results not only from its longevity, but also—despite the apparent decadence of most veterans—from its continued rapid growth into old age *(16)*.

Lower branches of giant sequoia die fairly readily from shading, but trees less than 100 years old retain most of their dead branches. Boles of mature trees generally are free of branches to a height of 30 to 45 m (98 to 148 ft) *(36)*.

Rooting Habit—During the first few years, the root system of giant sequoia seedlings consists of a taproot with few laterals—a habit that facilitates survival during dry summers *(36)*. The ratio of root length to shoot height during this period is about 2 to 2.5, with drier sites having higher ratios *(17)*. After 6 to 8 years, lateral root growth predominates, and elongation of the taproot practically stops *(36)*.

Roots of a mature tree commonly extend 30 m (100 ft) or more from the bole in well-drained soils, and occupy an area of 0.3 ha (0.7 acre) or more. Along drainage bottoms or edges of meadows, the radial extent of the root system may be no more than 12 to 15 m (40 to 50 ft). The largest lateral roots are usually no more than 0.3 m (1 ft) in diameter. Few roots extend deeper than 1 m (3 ft), and even less in areas with a high water table. Most of the abundant feeder roots are within the upper 0.6 m (2 ft) of soil. Concentrations of feeder roots often are high at the mineral soil surface *(16)*.

Immature trees, both in the groves and in older plantings, are notably windfirm *(20)*. Considering the shallowness of the root system and the great aboveground mass of large giant sequoias, it is remarkable that so many of these giants, especially leaners, remain standing for so long *(16)*.

Root grafting is common in giant sequoia *(16,36)*.

Reaction to Competition—Giant sequoia is shade intolerant throughout its life. Of its common coniferous associates, ponderosa pine is also intolerant, sugar pine is intermediate in tolerance, incense-cedar is intermediate to tolerant, and California white fir is tolerant *(17)*.

Fires or other disturbances that bare mineral soil and open the canopy characteristically benefit intolerant species, including giant sequoia, and move plant communities to earlier successional stages. In contrast, successful regeneration of giant sequoia in shade and in the absence of disturbance is less likely than that of any associated conifer *(17)*.

Once established, and with adequate light, young giant sequoias maintain dominance over competitors through rapid growth. In dense thickets, however, trees stagnate and recover slowly if released *(36)*. At maturity, giant sequoias are the tallest trees in the forest.

Although conspicuous in late successional communities dominated by California white fir, giant sequoia is not a true climax-stage species, because it fails to reproduce itself successfully in an undisturbed forest. Instead, mature trees are successional relicts because they live for many centuries while continuing to meet their light requirements by virtue of their emergent crowns *(16)*.

If various natural agents of disturbance—especially fire—operated freely, giant sequoia groves would consist of a roughly steady-state mosaic of even-aged groups of trees and shrubs in various stages of succession. The patchy nature of vegetational units would correspond to the pattern of disturbances. In the absence of disturbance, however, successional pathways converge toward a multilayered climax forest of pure California white fir *(4)*. In fact, since the advent of fire suppression, density of California white fir has increased markedly, while densities of early successional stage species have decreased *(26)*.

Damaging Agents—Fire is the most universal and probably most serious damaging agent of giant sequoia in its natural range *(36)*. Seedlings and saplings of giant sequoia, like those of most other tree species, are highly susceptible to mortality or serious injury by fire. However, in those locations most favorable for successful establishment and early growth—that is, mineral soil seedbeds and well-lighted openings—fuels tend to be sparser and to accumulate more slowly than in adjacent forested areas. The more vigorous seedlings and saplings thus may be large enough to survive a light fire by the time one occurs.

Larger giant sequoias, because of their thick nonresinous bark and elevated crowns, are more resistant to fire damage than associated species. Nevertheless, repeated fires over the centuries sear through the bark of a tree's base, kill the cambium, and produce an ever-enlarging scar. Almost all of the larger trees have fire scars, many of which encompass a large percentage of the basal circumference *(16)*. Few veterans have been killed by fire alone, but consequent reduction in supporting wood predisposes a tree to falling. Furthermore, fire scars provide entry for fungi responsible for root disease and heart rot *(29)*. Decayed wood, in turn, is more easily consumed by subsequent fires. The net result is further structural weakening of the tree. In addition, fire scars have been cited as the main cause of dead tops, so common in older trees *(35)*.

Lightning strikes, besides starting ground fires, sometimes knock out large portions of crowns or ignite dead tops. Mature trees seldom are killed by lightning, however *(16)*.

Old giant sequoias most commonly die by toppling. Weakening of the roots and lower bole by fire and decay is primarily responsible *(16,29)*. The extreme weight of the trees, coupled with their shallow roots, increases the effects of this weakening, especially in leaning trees. Other causative factors include wind, water-softened soils, undercutting by streams, and heavy snow loads *(16)*.

Although diseases are less troublesome for giant sequoia in its natural range than for most other trees, the species is not as immune to disease as once assumed *(1)*. Heartwood of downed sequoia logs is extremely durable, sometimes remaining largely intact for thousands of years. The heartwood of living trees, however, is less resistant to decay *(2)*. At least nine fungi have been found associated with decayed giant sequoia wood. Of these, *Heterobasidion annosum*, *Armillaria mellea*, *Poria incrassata*, and *P. albipellucida* probably are most significant *(29)*. The first two species also are serious root pathogens. Diseases generally do not kill trees past the seedling stage directly, but rather by contributing to root or stem failure. No other types of diseases, including seedling diseases, are known to be significant problems within the natural range of giant sequoia *(2)*. In nurseries and when planted outside its natural range, however, giant sequoia is highly susceptible to, and sometimes rapidly killed by, a number of organisms that may attack it at any stage from seedlings to mature trees *(1,25,39)*.

Insect depredations do not seriously harm giant sequoias older than about 2 years, although sometimes they may reduce vigor *(17)*. Carpenter ant (*Camponotus* spp.) galleries in decayed wood of tree bases evidently are not a direct cause of tree failure. Carpenter ants and other insects may facilitate the entry and spread of decay fungi, although the importance of such a role is not well known *(29)*. Like disease injury, damage by insects is more significant outside the tree's natural range.

Of various types of human impact on giant sequoia in the groves *(16,17,29)*, the most significant has been fire exclusion. The damage caused by fire is outweighed by its benefits in perpetuating the species. Fire is necessary to create and maintain conditions favorable for regeneration *(17)*. Furthermore, the elimination of frequent fires has permitted a large buildup of both dead and live fuels, and an associated increase in the potential for catastrophic crown fires. Agencies responsible for managing most of the groves currently have programs designed to reintroduce fire into giant sequoia ecosystems *(15,27,31)*.

Special Uses

Within its natural range, giant sequoia is valued primarily for esthetic and scientific purposes. Outside this range, it is highly regarded as an ornamental in several parts of the United States and in numerous other countries *(16)*. Some interest has been expressed for utilizing it in Christmas tree plantations.

Genetics

Population Differences

Isolation of the groves, or populations, of giant sequoia has existed sufficiently long for a number of population differences to become discernible. A recent study *(12)* found differences among populations on the basis of isozyme analyses, percent germination, and frequency distribution of cotyledon numbers. Levels of heterozygosity differed between the northern and southern parts of the range. Provenance tests in West Germany showed differences in cold hardiness and early growth among populations *(14,20,23)*. Bark pattern of mature trees varies among groves *(16)*. Somewhat surprisingly, however, genetic variability of giant sequoia is distinctly subdued when compared with that of other Sierra Nevada conifers and other trees in general *(21)*.

Races and Hybrids

No races of giant sequoia exist *(36)*. Fourteen horticultural forms are known, only two of which are common *(16)*.

Hybridization of giant sequoia with redwood has been reported in the Soviet Union but is unconfirmed in the western literature *(19)*.

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Taxodium distichum (L.) Rich. **Baldcypress**

Taxodiaceae **Redwood family**

T. distichum (L.) Rich. var. distichum **Baldcypress**

T. distichum var. *nutans* (Ait.) Sweet **Pondcypress**

L. P. Wilhite and J. R. Toliver

Baldcypress (*Taxodium distichum*) is a deciduous conifer that grows on saturated and seasonally inundated soils of the Southeastern and Gulf Coastal Plains. Two varieties share essentially the same natural range. Variety *nutans*, commonly called pondcypress, cypress, or black-cypress, grows in shallow ponds and wet areas westward only to southeastern Louisiana. It does not usually grow in river or stream swamps. Variety *distichum*, commonly called baldcypress, cypress, southern-cypress, swamp-cypress, red-cypress, yellow-cypress, white-cypress, tidewater red-cypress, or gulf-cypress, is more widespread and typical of the species. Its range extends westward into Texas and northward into Illinois and Indiana.

Pondcypress is less likely than baldcypress to have knees, and its knees are shorter and more rounded. Its fluted base tends to have rounded rather than sharp ridges and its bark usually is more coarsely ridged *(24)*. Its branchlets are more ascending than those of baldcypress *(44)*, but unfortunately it was given the varietal name *nutans* (nodding) from observation of a cultivated variation having drooping branches *(43)*. Typical specimens of pondcypress have nearly scale like leaves, which are appressed along the twig in several ranks. Seedlings and fast-growing shoots of pondcypress, however, often have disichous (two-ranked) leaves much like typical baldcypress foliage *(39)*. Despite the usual differences in appearance between the two varieties, not all specimens are typical, and it is often difficult and sometimes impossible to distinguish them *(44)*.

BALDCYPRESS

Habitat

Native Range

The native range of baldcypress (fig. 1) extends along the lower Atlantic Coastal Plain from southern Delaware to southern Florida and thence along the lower Gulf Coast Plain to southeastern Texas. Inland, baldcypress grows along the many streams of the middle and upper coastal plains and northward through the Mississippi Valley to southeastern Oklahoma, southeastern Missouri, southern Illinois, and southwestern Indiana *(31)*.

Climate

Humid, moist subhumid, and dry subhumid climatic types occur within the range of baldcypress. Normal precipitation increases from about 1120 mm (44 in) per year in southern Delaware and southern Illinois to about 1630 mm (64 in) along the central Gulf Coast, then decreases to about 760 mm (30 in) in southeastern Texas *(31)*. It should be noted, however, that baldcypress usually grows on intermittently flooded sites. Drainage, therefore, may be more important than rainfall in determining site suitability for baldcypress.

The growing season within the natural range of baldcypress increases from about 190 days in southern Illinois to virtually 365 days in southern Florida, and average annual minimum temperatures increase from about -18° C (0° F) to about 4° C (40° F) across this range *(31)*. Baldcypress trees planted in the Northeastern United States and southern Canada withstand minimum winter temperatures of -29° to -34° C (-20° to -29° F) *(23)*.

Thus, baldcypress can grow across a wide climatic range. Few seeds mature in the extreme northern

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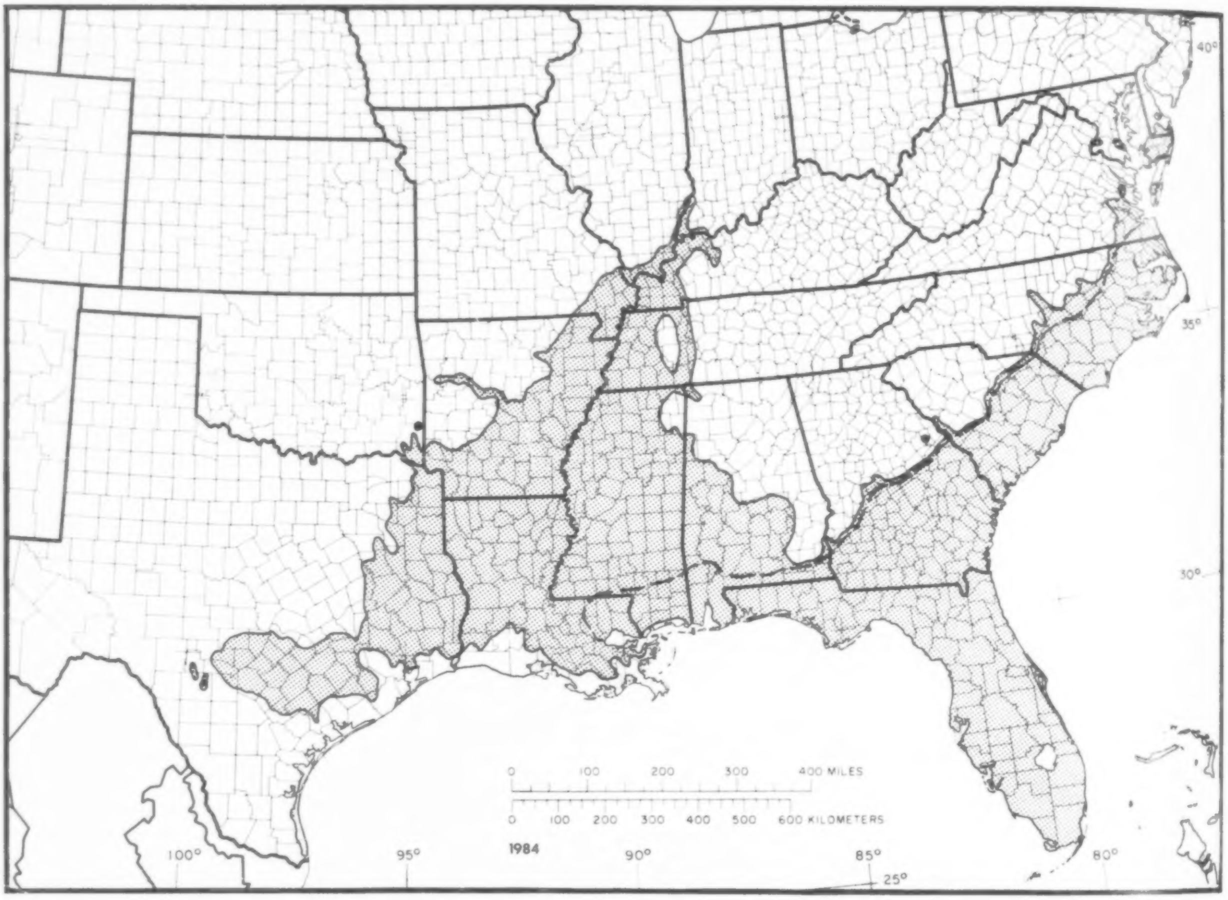

Figure 1—*The native range of baldcypress. The broken line indicates the northern limit of the variety* nutans, *pondcypress.*

part of the species' native range *(44)* however, and baldcypress grows best in warm climates *(28)*.

Soils and Topography

More than 90 percent of the natural baldcypress stands are on flat topography or in slight depressions at elevations of less than 30 m (100 ft) above sea level. The upper limit of its growth in the Mississippi Valley is at an elevation of about 150 m (500 ft). A few isolated stands occur at elevations of 300 to 530 m (1,000 to 1,750 ft) bordering deep hollows on the Edwards Plateau of Texas *(44)*. Because baldcypress usually grows on nearly flat topography, little is known about its growth in relation to topographic factors.

Baldcypress sites are characterized by frequent, prolonged flooding. Floodwaters may be 3 m (10 ft) deep or more and may flow at rates up to 6 km (4 mi) per hour or may be stagnant at times *(17)* (fig. 2).

Normally, baldcypress is found on intermittently flooded and very poorly drained phases of Spodosols, Ultisols, Inceptisols, Alfisols, and Entisols *(40)*. The native range of the species is in the thermic and hyperthermic soil temperature regimes.

On the Atlantic Coastal Plain, baldcypress grows best in the bottom lands of "red water" rivers, which originate in the Piedmont and mountains and during floods deposit a reddish, nutrient-rich silt into the bottom lands. Growth is poorer on the less fertile, coarser textured soils of the bottom lands of "black

Figure 2—*Baldcypress–tupelo swamp in a wildlife sanctuary maintained by the National Audubon Society, Dorchester County, SC.*

water" rivers, which originate in the Coastal Plain and are dark-colored with organic matter. Besides these alluvial soils, there are broad interstream areas of baldcypress swamps where soils range from heavy clays to coarse sand to mucks and peats, and where site quality is extremely variable *(41)*. Baldcypress also grows along estuaries near the coast but apparently cannot tolerate water containing more than 0.89 percent salt *(36)*. Stomatal conductance and net photosynthesis of 1-year-old baldcypress seedlings was reduced when salinity exceeded three ppt (.003 percent), indicating that salt water intrusion can adversely affect cypress at much lower concentrations *(37)*. Horticulturally, baldcypress can be grown on many upland soils, and it is seen in cities as a shade tree or ornamental.

Associated Forest Cover

Baldcypress is a dominant species in forest cover types Baldcypress (Society of American Foresters Type 101) and Baldcypress-Tupelo (Type 102). It is an associate species in Cabbage Palmetto (Type 74), Sweetgum-Willow Oak (Type 92), Black Willow (Type 95), Pondcypress (Type 100), Water Tupelo-Swamp Tupelo (Type 103), and Sweetbay-Swamp Tupelo-Redbay (Type 104) *(17)*.

Tree associates of baldcypress include water tupelo *(Nyssa aquatica)*, swamp tupelo *(N. sylvatica* var. *biflora)*, red maple *(Acer rubrum)*, sweetbay *(Magnolia virginiana)*, southern magnolia *(M. grandifolia)*, sweetgum *(Liquidambar styraciflua)*, and various oaks *(Quercus* spp.), ashes *(Fraxinus* spp.), and pines *(Pinus* spp.) *(2,29,46)*. Lesser vegetation associates include common buttonbush *(Cephalanthus occidentalis)*, poison-ivy *(Toxicodendron radicans)*, muscadine grape *(Vitis rotundifolia)*, Spanish moss *(Tillandsia usneoides)*, cattail *(Typha latifolia)*, lizardtail *(Saururus cernuus)*, and various hollies *(Ilex* spp.), viburnums *(Viburnum* spp.), lyonias *(Lyonia* spp.), sedges, grasses, and ferns *(2,44)*.

Baldcypress grows along streams that can deposit or remove soil to the extent that the soil surface, and consequently the depth to the water table, can fluctuate a few meters (several feet) during the life of a stand. Therefore, its understory and even arboreal associates can vary from species tolerant of prolonged flooding to species requiring well-drained conditions *(44)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Baldcypress is monoecious. Male and female strobili mature in one growing season from buds formed the previous year. The male catkins are about 2 mm (0.08 in) in diameter and are borne in slender, purplish, drooping clusters 7 to 13 cm (3 to 5 in) long that are conspicuous during the winter on this deciduous conifer. Pollen is shed in March and April. Female conelets are found singly or in clusters of two or three. The globose cones turn from green to brownish purple as they mature from October to December. The cones are 13 to 36 mm (0.5 to 1.41 in) in diameter and consist of 9 to 15 4-sided scales that break away irregularly after maturity. Each scale can bear two irregular, triangle-shaped seeds that have thick, horny, warty coats and projecting flanges *(19,39,44,45)*. Number of seeds per cone averages 16 and ranges from 2 to 34

(20). Cleaned seeds number from about 5600 to 18,430/kg (2,540 to 8,360/lb) *(39,44,45)*.

Seed Production and Dissemination—Some seeds are produced every year, and good seed crops occur at 3- to 5-year intervals *(45)*. At maturity, the cone scales with their resin-coated seeds adhering to them, or sometimes entire cones, drop to the water or ground *(42)*. This drop of mature seeds is often hastened by squirrels, which eat baldcypress seeds but usually drop several scales with undamaged seeds still attached from each cone that they pick *(5)*. Floodwaters spread the scales or cones along streams and are the most important means of seed dissemination *(44)*.

Seedling Development—Germination is epigeal *(45)*. Under swamp conditions, germination generally takes place on a sphagnum moss or a wet-muck seedbed. Seeds will not germinate under water, but some will remain viable for 30 months under water. On the other hand, seeds usually fail to germinate on better drained soils because of the lack of surface water. Thus, a soil saturated but not flooded for a period of 1 to 3 months after seedfall is required for germination *(44)*.

After germination, seedlings must grow fast enough to keep at least part of their crowns above floodwaters for most of the growing season *(10,12,13)*. Baldcypress seedlings can endure partial shading but require overhead light for good growth *(49)*. Seedlings in swamps often reach heights of 20 to 75 cm (8 to 30 in) their first year *(7)*. Growth is checked when a seedling is completely submerged by flooding, and prolonged submergence kills the seedling *(44)*.

In nurseries, *Taxodium* seeds show an apparent internal dormancy that can be overcome by various treatments that usually include cold stratification or submerging in water for 60 days *(19)*. Nursery beds are sown in spring with pretreated seeds or in fall with untreated seeds *(45)*. Seedlings usually reach 75 to 100 cm (30 to 40 in) in height during their first (and usually only) year in the nursery *(49)*. Average size of 1-0 nursery-grown seedlings in a seed source test including 72 families was 81.4 cm (32 in) tall and 1.1 cm (0.43 in) in diameter *(19)*.

Control of competing vegetation may be necessary for a year or more for baldcypress planted outside of swamps. Five years after planting baldcypress on a harrowed and bedded poorly drained site in Florida, survival was high but heights had increased only 30 cm (12 in), probably because of heavy herbaceous competition *(25)*. Seedlings grown in a crawfish pond in Louisiana, where weed control and soil moisture were excellent through June, averaged 2.9 m (9.7 ft) and 3.5 cm (1.4 in) d.b.h. after 5 years. However, a replicate of the same sources planted on an old soybean field, where weed control and soil moisture were poor, resulted in the same d.b.h. but a smaller average seedling height of 2.1 m (7.0 ft) *(John R. Toliver, unpublished data)*. When planted in a residential yard and weeded and watered averaged 3.7 m (12 ft) tall 3 years later *(49)*.

Vegetative Reproduction—Baldcypress is one of the few conifer species that sprouts. Thrifty sprouts are generally produced from stumps of young trees, but trees up to 60 years old also send up healthy sprouts if the trees are cut during the fall or winter. However, survival of these sprouts is often poor and those that live are usually poorly shaped and do not make quality sawtimber trees *(10,13,38)*. Stumps of trees up to 200 years old may also sprout, but the sprouts are not as vigorous and are more subject to wind damage as the stump decays *(44)*. In the only report on the rooting of baldcypress cuttings found in the literature, cuttings from trees 5 years old rooted better than those from older trees *(30)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Baldcypress is reputed to be slow growing and very long-lived, but during some growing seasons, perhaps in response to soil-moisture fluctuations, many baldcypress appear to produce more than one ring of stemwood. Counting these false rings in with true annual rings has led to overestimations of ages and consequently to underestimations of growth rates.

A study in three baldcypress plantations of known age revealed that on increment cores under magnification, true latewood appeared as narrow bands of small, thick-walled cells, and the stains that cause false latewood tended to disappear. The larger trees in the study had more apparent rings than smaller trees of the same age, and conventional ring counts averaged about 1.6 times the actual age *(44)*.

Many years before that study, an investigator having no trees of known age to confirm his age counts, but stating that he could distinguish the stains of false latewood from true latewood bands, concluded that trees 400 to 600 years old were common in many virgin stands of baldcypress and that a few trees reached about 1,200 years *(44)*.

Under forest conditions, baldcypress stems generally require about 200 years to reach sufficient size to yield a high proportion of heartwood lumber *(28)*. Also at about age 200, height growth ceases *(44)*. After this age many baldcypress slowly die back from the top as a fungus-caused rot progresses downward through the stem.

Baldcypress is noted for the large size it can attain (fig. 3). In virgin forests, the largest trees were 215 to 365 cm (84 to 144 in) in d.b.h. and 43 to 46 m (140 to 150 ft) in height *(44)*. In the 1982 "National Register of Big Trees," the champion baldcypress, which grows in Louisiana, was reported to be 520.7 cm (205 in) in d.b.h. and 25 m (83 ft) tall *(1)*.

Baldcypress also is noted for its high merchantable yields. In virgin stands, yields of 112 to 196 m3/ha (8,000 to 14,000 fbm/acre) over tracts hundreds of hectares in extent were common, and some stands likely exceeded 1400 m^3/ha (100,000 fbm/acre). One tree in Okefenokee Swamp in Georgia scaled 168 m^3 (12,000 fbm) *(44)*.

Some second-growth stands are approaching the yields of the best virgin stands. A 96-year-old stand in Mississippi contained 980 m^3/ha (70,000 fbm/acre) and its crop trees averaged 36.3 m (119 ft) tall *(49)*. A 63-year-old second-growth stand in Louisiana averaged 1,260 cypress and 258 swamp tupelo trees per hectare, respectively (504 and 103/acre), resulting in volumes of 409 and 107 m^3/ha (6,356 and 1,423 ft^3/acre), respectively *(15)*.

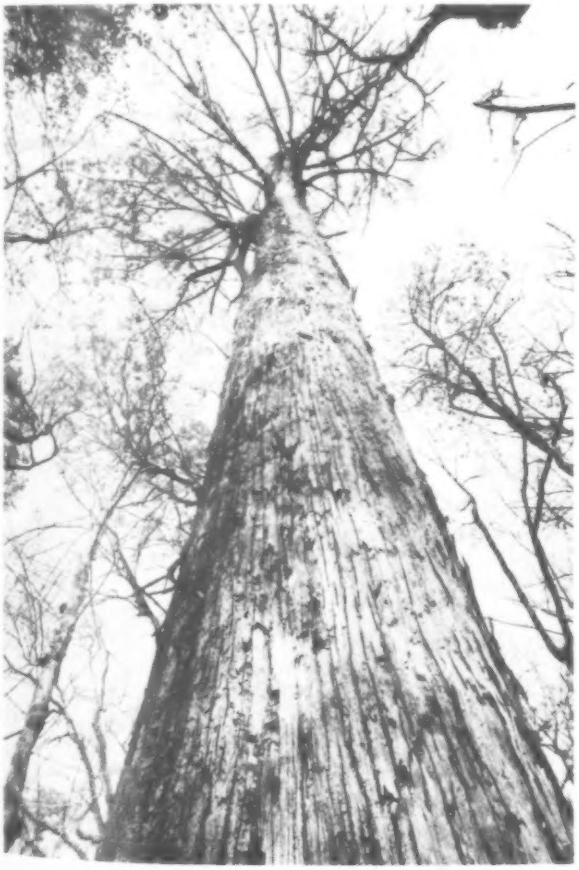

Figure 3—*Virgin baldcypress in Dorchester County, SC.*

The sample is limited, but some plantations, at least, grow faster than natural stands. In Mississippi, one plantation established on abandoned cropland had dominants averaging 21 m (69 ft) tall at 41 years *(49)*, and another plantation that had been cultivated or mowed for the first 10 years contained 175 m^3/ha (2,333 ft^3/acre) at age 31 and the 30 largest trees averaged 21.6 m (72 ft) tall and 36 cm (14.2 in.) d.b.h. Ten-year volume growth (from age 21 to 31 yrs) of the trees in this plantation was 77.5 m^3/ha (1,033 ft^3/acre) *(29)*.

Baldcypress grows well at high stand densities. From age 60 to 70 years, a baldcypress-hardwood stand in Florida increased from 39 to 43 m^2/ha (168 to 189 ft^2/acre) in basal area and from 359 to 428 m^3/ha (57 to 68 cords/acre) in volume. The baldcypress grew at a faster rate than the tupelo and sweetgum. Thinning plots within the stand to various densities at age 60 resulted in faster growth of individual crop trees, but in slower growth per unit area than for the unthinned part of the stand *(33)*.

Density was even higher in a second-growth stand of baldcypress in Mississippi: 61 m^2/ha (265 ft^2/acre) at age 78. Thinning that stand to 46 m^2/ha (200 ft^2/acre) increased growth through age 96 more than did no thinning or a heavier thinning *(49)*. Volume growth of a 63-year-old second-growth stand in Louisiana, with an average density of 50 m^2ha (220 ft^2/acre) in basal area, was 54 m^3/ha (716 ft^3/acre) over a 5-year period. Crown thinning in this stand increased diameter growth and appeared to increase sawtimber volume per hectare after 5 years. Heavier thinning intensities stimulated epicormic branching on many trees, which could lower log quality. However, the largest dominant crop trees were least affected by epicormic branching *(15)*.

Cypress swamps and other forested wetlands that receive periodic nutrient subsidies from floodwaters probably are some of the world's most productive ecosystems. The annual above-ground production of biomass in a baldcypress-ash floodplain forest in Florida was 15 700 kg/ha (14,000 lb/acre) *(4)*. In comparison, terrestrial forest communities in the temperate region often produce 12 300 to 15 000 kg/ha (11,000 to 13,400 lb/acre) annually *(11)*.

Stillwater forested wetlands do not receive nutrient subsidies from floodwaters, and they have production rates comparable to, or lower than, those of terrestrial forests. Such wetlands, however, offer additional benefits such as storage of water and peat *(4)*.

Rooting Habit—Baldcypress seedlings develop a taproot *(49)*, and at least some planted baldcypress up to 25 cm (10 in) in d.b.h. maintain taproots *(43)*. Older, naturally seeded baldcypress in swamps develop several descending roots that provide anchorage, and numerous lateral roots from which rise peculiar conical structures known as "knees" *(23)*. These knees vary in height from several centimeters to more than 3.7 m (12 ft), depending apparently upon the average water level of the site *(44,47)*. Knees are less likely to form in absence of flooding or where permanently standing water is 30 cm (12 in) or more in depth *(48)*. However, small knees have been observed on many trees not subjected to flooding *(3)* and it is not uncommon for ornamental trees to produce knees. Research has found no physiological function for cypress knees. They may be beneficial as aeration organs but are not of critical importance to survival *(17)*. Knees may also help to anchor trees because they develop large masses of roots.

The extensive root system along with a buttressed base make baldcypress windfirm in soft, wet soils. Even winds of hurricane force rarely overturn them *(44)*.

Reaction to Competition—The relative shade-tolerance of baldcypress has not been definitely established. Seeds often germinate in heavily shaded places but usually do not survive or develop into large trees *(10,13)*. Most successful stands regenerate in large openings. The species grows slowly in partial shade but the best growth occurs with full overhead light. For these reasons, intermediate shade tolerance seems the most appropriate classification. In fully stocked stands baldcypress characteristically has a clean, smooth stem and small crown, readily pruning itself of branches, but in poorly stocked stands it is very limby *(44)*.

Damaging Agents—A fungus, *Stereum taxodi*, that causes a brown pocket rot known as "pecky cypress" attacks the heartwood of living baldcypress trees, especially the overmature ones. The fungus most frequently gains entrance in the crown and slowly works downward, sometimes destroying a considerable part of the heartwood at the base of the tree. The action of the fungus ceases when the tree is felled. The durability of baldcypress lumber, so far as is known, is not affected by the presence of pecky material *(28,44)*.

A few other fungi attack the sapwood and heartwood of baldcypress and a few needle and twig fungi have been reported, but none of these is known to cause serious damage *(26)*.

Several insects attack baldcypress, but damage is generally minor *(21)*. However, the fruit tree leafroller, *(Archips argyrospila)*, previously unreported on baldcypress, became epidemic in 1983, in the lower Atchafalaya Basin and adjoining drainages to the east and south in Louisiana. The leafroller larvae commence webbing and feeding on cypress needles as soon as buds break and small leaflets expand. Large-scale killing of trees has not been observed, but those suffering repeated leafroller defoliation show die-back. Mortality of pole-sized trees has been linked to defoliation *(21)*.

The cypress flea beetle *(Systena marginalis)* causes discoloration of foliage and the cypress looper *(Anacamptodes pergracilis)* causes defoliation *(44)*. Another common defoliator is the bagworm *(Thyridopteryx ephemeraeformis) (42)*. The southern cypress bark beetle *(Phloeosinus taxodii)* tunnels beneath the bark of limbs and trunks *(27)*. The baldcypress coneworm *(Dioryctria pygmaeella)* is a serious pest of cones of baldcypress and pondcypress, capable of destroying more than 75 percent of a single year's crop *(34)*.

Nutria *(Myocastor coypu)* often clip or uproot newly planted cypress seedlings before the root systems are fully established, thus killing the seedlings *(12)*. Where high nutria populations occur, entire plantings are often destroyed in a few days. The Soil Conservation Service recommends cessation of baldcypress planting until control measures are found. To date, the only successful control has been placement of a chicken wire guard around each seedling *(12)*. Deer and swamp rabbits clip seedlings above the ground and eat the tender stems and branches, but these seedlings generally resprout and continue to grow *(18,44)*.

Special Uses

The unusual and pleasing appearance of baldcypress—its knees, buttressed base, massive bole, and irregular crown often festooned with Spanish moss—has led to its introduction as an ornamental in many parts of the world *(3,45)*.

Baldcypress seeds are eaten by wild turkeys, squirrels, evening grosbeaks, and wood ducks *(6)*; they are a minor part of the diet of other waterfowl and wading birds *(32)*; and they were an important food for the now-extinct Carolina parakeet *(6)*. Large old baldcypress furnish unique habitats for some wildlife. Bald eagles and ospreys nest in the tops.

Yellow-throated warblers forage in the Spanish moss or resurrection fern *(Polypodium polypodioides)* often found on old trees. Prothonotary warblers achieve their highest densities in baldcypress-tupelo stands where they find nesting cavities in old decaying baldcypress knees. Catfish spawn in submerged hollow cypress logs *(22)*.

Baldcypress wood has a multitude of uses and is well known for its ability to resist decay. Cypressene, an oil extracted from the wood, is believed to give baldcypress high decay resistance. Older baldcypress, particularly old-growth, virgin trees growing in the deep swamps, is known as tidewater redcypress and is considered to be very resistant to rot *(3)*. For this reason, cypress wood has long been favored in the building construction, fences, planking in boats, river pilings, furniture, interior trim, cabinetry, sills, rafters, siding, flooring and shingles, garden boxes, greenhouses, and many other uses *(3)*. However, second-growth baldcypress lack the decay resistant heartwood of the old-growth trees *(8,9)*. At what age or size decay resistance develops is unknown, but wood from trees at least 63 years old is susceptible to rot *(9)*. Caution is recommended in the use of lumber from these trees in exposed situations, and the wood should be treated if rot resistance is essential *(3,9)*. Pecky cypress, caused by the fungus *Stereum taxodii*, is used in products where durability rather than water tightness is required, and in decorative wall paneling *(14,28)*.

Riverine swamps of baldcypress cause floodwaters to spread out, slow down, and infiltrate the soil. Thus, these stands reduce damage from floods and act as sediment and pollutant traps *(46)*.

Genetics

Recognized varieties of baldcypress are indicated in the introduction to this report. Baldcypress grows across a range of wetland sites and over a wide geographic area, however, so other races may exist. A cultivar, 'Pendens', having pendulous branches, has been developed *(50)*. In Russia, hybridization of baldcypress with redwood *(Sequoia sempervirens)* has been reported *(44)*.

Genetic variation of baldcypress seed, cone, and nursery-seedling growth was explored in two geographic seed source studies incorporating seed collected along the Mississippi River flood plain from Illinois to Louisiana. Variation among seed sources and families-within-source was of significant magnitude to indicate a potential for genetic selection and gain in growth. However, no specific pattern of variation was noted *(18,19,20)*.

PONDCYPRESS

Habitat

Native Range

Pondcypress grows from southeastern Virginia to southern Florida to southeastern Louisiana (fig. 1) and almost always at elevations below 30 m (100 ft).

Climate

Humid and moist subhumid climatic types occur within the range of pondcypress. Normal precipitation increases from about 1220 mm (48 in) per year in southeastern Virginia to 1630 mm (64 in) along the east Gulf Coast. The growing season increases from about 240 days in southeastern Virginia to about 300 days in southeastern Louisiana to virtually 365 days in southern Florida. Average annual minimum temperatures increase from about -12° C (10° F) in southeastern Virginia to 4° C (40° F) in southern Florida *(31)*.

Soils and Topography

Pondcypress grows on the very poor and poorly drained phases of Spodosols and Ultisols *(40)* of the thermic and hyperthermic soil temperature regimes. Soils range from sands to clays to mucks to peats.

Pondcypress occupies the shallow ponds and poorly drained areas of the Coastal Plain and rarely grows in the river and stream swamps as does baldcypress *(44)*. There is evidence that pondcypress does not grow on soils with a pH above 6.8 and bald cypress does not grow on soils with a pH below 5.5 *(35)*, but it is not known if the range in which both grow might be narrower than pH 5.5 to 6.8.

Pondcypress sites in general are much less fertile than baldcypress sites. Pondcypress grows on more acid soils, and it seldom grows on sites that receive periodic subsidies of nutrients from floodwaters.

Pondcypress stands almost always are found on flat topography or in slight depressions often called domes *(16)*; therefore, little is known concerning growth of pondcypress in relation to higher topographic features.

Associated Forest Cover

Pondcypress is the dominant species in the forest cover type Pondcypress (Society of American Foresters Type 100) *(17)*. It is an associate species in Longleaf Pine-Slash Pine (Type 83), Slash Pine (Type 84), Slash Pine-Hardwood (Type 85), Pond Pine (Type

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98), Baldcypress (Type 101), Water Tupelo-Swamp Tupelo (Type 103), and Sweetbay-Swamp Tupelo-Redbay (Type 104).

The most common sites for pondcypress are the shallow ponds of the Coastal Plain (fig. 4). Here, its chief tree associate is swamp tupelo. Along the margins and on slightly elevated positions within the ponds, associates are pines *(Pinus* spp.), red maple, sweetbay, and loblolly-bay *(Gordonia lasianthus)*. Lesser vegetation associates include common buttonbush, yaupon *(Ilex vomitoria)*, swamp cyrilla *(Cyrilla racemiflora)*, viburnums, swamp privet *(Forestiera acuminata)*, southern bayberry *(Myrica cerifera)*, bitter gallberry *(Ilex glabra)*, ferns, and vines *(17)*.

In addition to growing in the ponds of the Coastal Plain, pondcypress is found in some of the swamps along "black water" rivers and creeks, in Carolina bays, in the Okefenokee Swamp, and in pondcypress savannahs. On these various sites, associates of pond cypress include most of those listed above plus many others *(2,46)*.

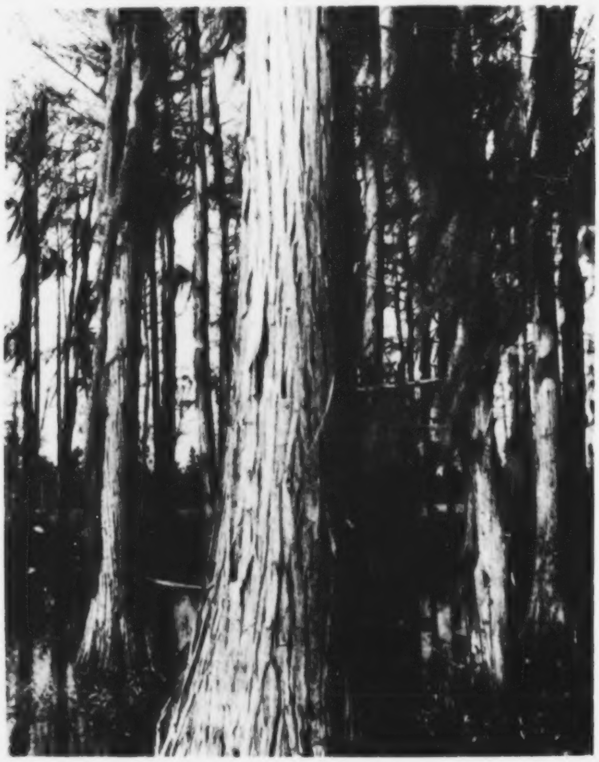

Figure 4—*Pondcypress trees near Gainesville, FL.*

Life History

Reproduction and Early Growth

A sample of pondcypress seeds numbered 8 900/kg (4,040/lb) *(45)*. Generally, the flowering characteristics, seeds, seeding habits, vegetative reproduction, and reaction to competition appear to be similar to those of baldcypress. Trees are monoecious, seeds are distributed by gravity and water, germination is epigeal, and the species is capable of sprouting and is classed as intermediate in its tolerance to shade. In shallow ponds, both soil and water conditions appear singularly favorable for pondcypress seed germination and early growth, for here natural reproduction is almost always uniformly abundant *(44)*.

Sapling and Pole Stages to Maturity

In the 1982 "National Register of Big Trees," the champion pondcypress, which grows in Georgia, was reported to be 229 cm (90 in) in d.b.h. and 41.1 m (135 ft) tall *(1)*. This is approaching the size of the larger baldcypress. Such giants, however, are much more rare among pondcypresses than among baldcypresses. Although little information is recorded about the growth rate of pondcypress, general observations indicate that the tree does not attain the age and large size of baldcypress, nor does it grow as fast. The smaller size and slower growth of pondcypress may be inherent but are also attributable to the poor site conditions under which the tree usually grows *(44)*.

Because of its generally thicker bark, pondcypress is more resistant to fire than baldcypress *(24)*.

Special Uses

Lumbermen commonly cut and sell pondcypress and baldcypress timber together without distinguishing between them *(28)*.

Pondcypress ponds, domes (or heads), and savannahs provide the only breeding opportunity for a number of tree frogs, toads, and salamanders; provide nesting sites and habitats for herons, egrets, and many other birds; and are watering places for the birds, mammals, and reptiles of the surrounding pinelands. These wet areas serve as recharge areas for surface aquifers, and research has shown that pondcypress domes can serve as tertiary sewage treatment facilities in improving water quality, recharging ground water, and possibly increasing pondcypress growth rates *(46)*. Functions of these domes and cypress swamps are discussed in depth in the book "Cypress Swamps" *(16)*.

Genetics

There are no known hybrids of pondcypress.

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Taxus brevifolia Nutt. Pacific Yew

Taxaceae Yew family

Charles L. Bolsinger and Annabelle E. Jaramillo

Pacific yew *(Taxus brevifolia)*, also called western yew, is a coniferous tree associated with several conifer and hardwood tree species on a variety of sites. Pacific yew tolerates shade, and in undisturbed stands is usually found as an understory tree. Growth of such trees is slow, but where the overstory has been removed or thinned, diameter growth on undamaged yew trees may increase considerably. Pacific yew rarely exceeds 60 cm (24 in) in d.b.h., and 15 m (49 ft) in height. The largest on record is 142 cm (56 in) in d.b.h., and 18 m (60 ft) in height *(28)*. The wood is hard, heavy, and resistant to decay. Although not of great interest to the forest products industry, it has many special uses. The bark of Pacific yew contains a drug, taxol, that is being used in cancer research, so demand for yew bark by the National Cancer Institute has increased dramatically in recent years *(9)*.

Habitat

Native Range

Pacific yew (fig. 1) grows in forests from the southern tip of southeast Alaska—including Annette and Prince of Wales Island—south through the Pacific Coast region of British Columbia, Vancouver and the Queen Charlotte Islands, and the Olympic Peninsula of Washington. It is rare in the Coast Range south of the Olympic Peninsula in Washington and north of the Umpqua River in Oregon, but occurs with greater frequency in the Coast Range in southern Oregon and northern California. Isolated occurrences are found as far south as Marin and San Mateo Counties in California. Yew occurs in scattered localities in the valleys between the Coast Range and Cascade Ranges of Oregon and Washington. In the Cascade Range, it is fairly common at low to moderate elevations, and on some sites in southern Oregon it is abundant. Pacific yew extends south through the Klamath Mountains of California, then southeasterly to the western slopes of the Sierra Nevada. Its southern limit is in Calaveras County. Farther inland, it grows on the western slopes of the Rocky Mountains in British Columbia, south into northern Idaho and western Montana, the Lewis Range in Montana, and isolated areas in eastern Washington and northeastern Oregon. In the South Fork of the Clearwater River basin in Idaho, Pacific yew deviates from its role as a minor forest component and becomes a dominant on about 16 000 hectares (40,000 acres) *(8,19,20,27,30,31,35,40,42,43,44,47,49)*.

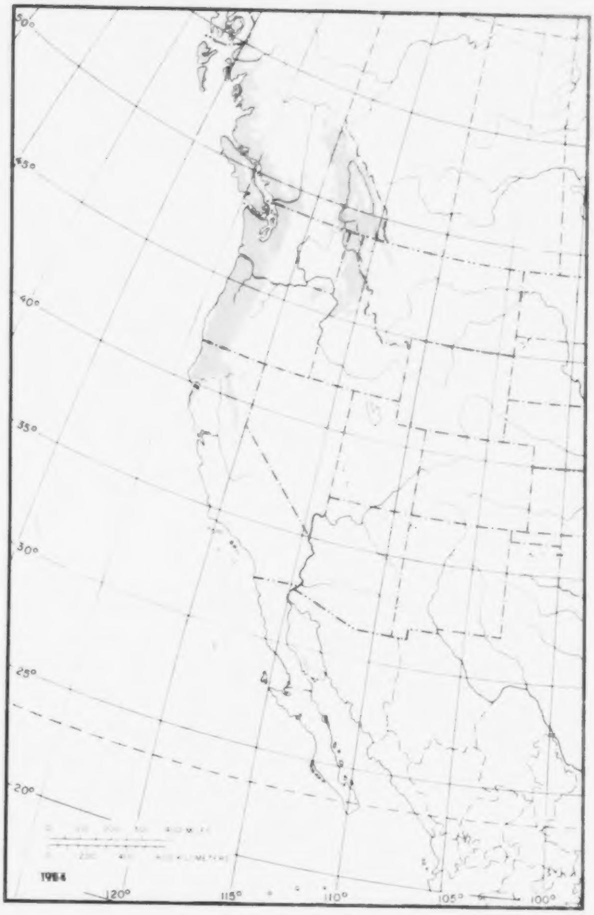

Figure 1—*The native range of Pacific yew.*

Climate

Pacific yew is found over a wide range of moisture and temperature conditions *(8,11,19,35,40,44)*. In dry, subhumid areas with an average annual precipitation as low as 470 mm (19 in), it is confined to

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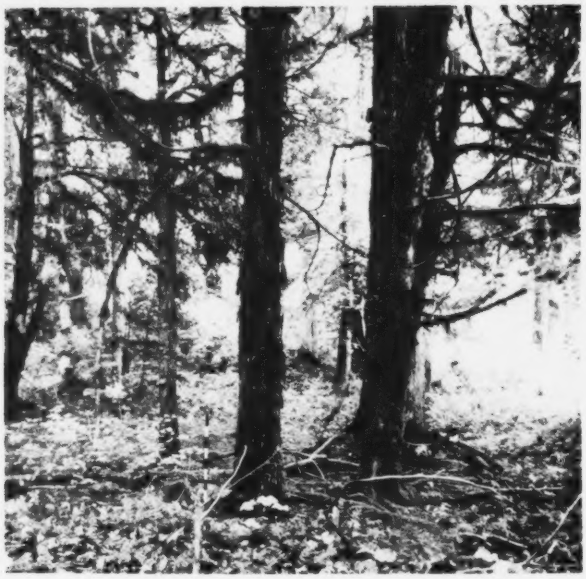

Figure 2—*Understory of Pacific yew trees, Wind River Research Natural Area near Carson, WA.*

streamside areas and the lower third of north-facing slopes. Some large specimens can be found in such environments; for example, the largest known yew tree in Idaho—84.8 cm (33.4 in) d.b.h. and 8.5 m (28 ft) tall—is at the bottom of Hell's Canyon in an area that receives about 500 mm (20 in) of precipitation annually *(21)*. On the Queen Charlotte Islands, Pacific yew is confined to the borders of inlets *(44)*. Throughout much of its range within humid and superhumid forests (precipitation of 1400 to 4000 mm [55 to 157 in]), it can be found on all slopes, benches, and ridgetops. For example, a large yew tree in Oxbow County Park near Troutdale, Oregon (precipitation about 1450 mm [57 in]), is on the highest point in the park, a 210-m (690-ft) ridge overlooking the Sandy River 168 m (550 ft) below *(3)*. Pacific yew is found from sea level in coastal areas to 2440 m (8,000 ft) in the Sierra Nevada. Length of growing season ranges from 60 to 300 days, with annual minimum temperatures from −15° to −12° C (5° to 10° F) *(4,8,11,24,25,35,45)*.

Soils and Topography

Pacific yew grows best on deep, moist or rich, rocky or gravelly soils. In dry interior forests, the species develops best along mountain streams, and in shady canyons, ravines, and coves. Within the moist maritime climate of the Pacific Northwest, it grows most abundantly in drier, warmer environments. A partial list of soils on which Pacific yew grows includes those in the orders Ultisols, Alfisols, and Inceptisols *(4,11,20,24,25,27,30,37,45,50)*.

Associated Forest Cover

Pacific yew commonly occurs as an understory species (fig. 2) in several forest cover types. It is a major component in some stands, but in most it is minor to rare. In some types, it tends to be found mostly on microsites. Some examples: In stands of ponderosa pine *(Pinus ponderosa)*, grand fir *(Abies grandis)*, and western larch *(Larix occidentalis)* in the drier interior forests, yew is found in moist areas near streams and springs (but on well drained soil); on wet, hummocky sites west of the Cascades, yew can be found in Oregon white oak *(Quercus garryana)*—Oregon ash *(Fraxinus latifolia)* stands (ash occupies the low, wet spots and yew grows with the oak on slightly raised hummocks); scattered large yew trees grow along the Clackamas River in northwest Oregon on berms and banks between first and second bottomlands in stands of black cottonwood *(Populus trichocarpa)*, red alder *(Alnus rubra)*, hawthorn (*Crataegus* spp.), crab apple (*Malus* spp.), and willow (*Salix* spp.) *(3,47)*. By far, Pacific yew is most common in dense conifer forests. Among the major Society of American Foresters (16) cover types in which Pacific yew is found are: Engelmann Spruce-Subalpine Fir (206), Interior Douglas-Fir (210), White Fir (211), Grand Fir (213), Black Cottonwood—Willow (222), Western Hemlock (224), Western Redcedar—Western Hemlock (227), Western Redcedar (228), Pacific Douglas-Fir (229), Douglas-Fir—Western Hemlock (230), Port-Orford-Cedar (231), Redwood (232), Oregon White Oak (233), Douglas-Fir—Tanoak—Pacific Madrone (234), Sierra Nevada Mixed Conifer (243), and Pacific Ponderosa Pine—Douglas-Fir (244) *(4,8,11,17,24,25,35,45,47)*.

In western Oregon, Douglas-fir was present on 89 percent of the forest inventory plots in which yew was tallied. A list of plants found most frequently with Pacific yew on these plots (table 1) indicates the broad range of conditions to which the species can adapt.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Pacific yew is dioecious. Male strobili are stalked, budlike, pale yellow, and composed of 6 to 12 filamentous stamens, each with 5 to 9 anthers. They are abundant on the un-

Table 1—Plants frequently found on plots with Pacific yew present, western Oregon.

Species	Percentage of plots	Indicator value [1]
Pseudotsuga menziesii	89	Common
Berberis nervosa	75	Common
Polystichum munitum	75	Mesic, common
Acer circinatum	70	Common
Tsuga heterophylla	59	Cool, common
Gaultheria shallon	59	Warm, mesic to dry
Corylus cornuta var. *californica*	43	Warm, dry
Acer macrophyllum	39	Warm
Vaccinium parvifolium	39	Warm, common
Thuja plicata	36	Moist, common
Alnus rubra	36	Warm, moist
Rhododendron macrophyllum	34	Cool, mesic
Cornus nuttallii	32	Warm, dry
Holodiscus discolor	27	Hot, dry
Linnaea borealis	27	Mesic
Arbutus menziesii	25	Warm, dry
Abies grandis	23	Warm, dry
Xerophyllum tenax	23	Cool, dry
Rhus diversiloba	20	Hot, dry
Oxalis oregana	20	Warm, moist

[1] Based on information from *4,24*, and *45*.

derside of branch sprays and usually appear in May or June. Female strobili are less abundant, greenish, and composed of several scales. They also are borne on the underside of branches. The fruit is an ovoid-oblong seed about 8 mm (0.3 in) long, partially enveloped by a fleshy, berrylike, scarlet, cup-shaped disk called an aril. Pollen is dispersed by wind in the spring *(6,11,19,22)*.

Seed Production and Dissemination—Fruits ripen from August to October of the same year that flowering occurs. Fruits either drop to the ground or are taken from trees by birds or rodents. Birds devour the fleshy arils and void the seeds which remain viable. Chipmunks and squirrels often take only the seeds. Rodents and some birds—nuthatches, for example—cache yew seeds, thus creating the clusters of yew seedlings observed in some areas *(11)*. The seed is about 6 mm (0.24 in) long with a depressed hilum, bony inner coat, and membranous outer seedcoat. Pacific yew is a prolific seeder *(19,43)*. Seeds average about 33,100/kg (15,000/lb) after cleaning *(39)*. The frequency of good seed crops is unknown.

Seedling Development—Seeds of Pacific yew germinate slowly and require stratification. Germination tests indicate that 30° C (86° F) day and 20° C (68° F) night temperatures are desirable *(11,19,43)*. Germination is epigeal, and usually in heavy organic matter. In a study in Idaho, wild yew seedlings were distributed in seedbeds as follows *(11)*:

Type of seedbed	Percentage of seedlings
Forest litter	61
Decaying wood	20
Bird and rodent caches	16
Mineral soil	3
	100

Yew seeds sown in nursery beds in late spring require mulching. Beds require shading during the summer and again in December. Some seeds do not germinate until the second spring after sowing *(39)*.

Vegetative Reproduction—Pacific yew is capable of layering and often sprouts from stumps or rootstocks after the top has been killed or the tree cut *(3,11,23,44)*. Layering usually occurs after branches or tree tops have been pressed to the ground for a prolonged period by large fallen trees or limbs (11), although occasional old yew trees can be found surrounded by a ring of well rooted branches that were apparently held down only by their own weight and the weight of snow in the winter.

Although Pacific yew is sensitive to heat *(11,26,44)*, sprouts that originated from the bases of burned stumps were reported from the Rogue River National Forest in southern Oregon *(23)*. Young yew trees that originated by layering and sprouting were observed in a sunny, south-facing clearcut on the Mount Hood National Forest in northern Oregon. From one cut yew tree with a stump diameter of 30 cm (12 in), seven new trees had originated by layering before cutting, and a clump of vigorous stump sprouts had originated after cutting. Sprouts emerged from one side of the 36-cm-high (14 in) stump (the opposite side had been debarked during logging) from ground level to the top. The layers were 1.0 m to 2.5 m (3 ft to 8 ft) from the stump. Most of the layers had been damaged by logging and lacked the vigor of the stump sprouts (3).

Sapling and Pole Stages to Maturity

Growth and Yield—Pacific yew, unlike most woody plants that grow in heavily shaded forest understories, often has a straight bole (see fig. 2). Although yew trees are reported to have typically fluted, ridged, and asymmetrical trunks, often with tightly spiraled grain *(6,11,23,37,44)*, yew cutters in southwest Oregon reported that many yew trunks were round and unfluted above the base section, and straight-grained *(7)*. Large limbs are common in the mid and upper bole. The crown tends to be ragged and lopsided. Pacific yew "reaches" for light by way of limbs that may be as long as the tree is tall. Young trees often have an umbrella-shaped crown of flat branches, and old trees have long drooping spraylike branches. Pacific yew is sometimes shrublike, forming dense thickets. In western Montana, parts of Idaho, northeastern California, the Blue Mountains of eastern Oregon and southeastern Washington, and at high elevations throughout its range, the shrub form of yew often occurs in the absence of tree-size specimens *(3,8,10,11,20,27,30,31,35,44,49,50)*. In other areas, large tree-size yews may occasionally be found in or near yew shrub thickets (3). Whether the differences in size and form are genetic traits or the results of environment and stand history is not known.

The needles of Pacific yew are dark green on the underside, two ranked, and spirally arranged on twigs. The bark is purplish, papery thin, and scalelike. New bark is rose red *(6,19,22,40)*. The wood is fine grained, hard, and heavy: at 712 kg/m^3 (about 44 lb/ft^3) (8 percent moisture content), it is the heaviest of U.S. conifers, comparable in weight to high-density hardwoods such as ash, oak, and hard maple *(46)*. Heartwood is red to brownish red, and sapwood is whitish yellow to bright yellow.

Pacific yew grows slowly, taking about the same time to grow to 30 cm (12 in) in d.b.h. as other conifers in the same stand take to grow to several times that size. Height growth is correspondingly slow. Trees larger than 50 cm (20 in) in d.b.h. and taller than 12 m (40 ft) are rare within most of the species' range: they account for less than 2 percent of the yew trees tallied on inventory plots on non-Federal land in California, Oregon, and Washington. The following tabulation shows average height by diameter class as determined from 55 Pacific yew trees randomly selected in Oregon and Washington *(47)*:

D.b.h.	Total height
10 cm (4 in)	6 m (20 ft)
20 cm (8 in)	8 m (26 ft)
30 cm (12 in)	10 m (31 ft)
40 cm (16 in)	11 m (37 ft)
50 cm (20 in)	13 m (43 ft)
60 cm (24 in)	15 m (49 ft)

Because of the slow growth of individual trees and because the species is typically found as an occasional tree in stands of other tree species, volumes and yields of Pacific yew are low. Stands with 125 yew trees/ha (50/acre) that are 20 cm (8 in) in d.b.h. and larger have been observed, but always in association with other species *(3)*. The theoretical volume of yew wood in such stands could be as much as 140 m^3/ha (2,000 ft^3/acre), including the volume in main stems from ground level to tip. The greatest volume of Pacific yew found in randomly located plots on non-Federal land in California, Oregon, and Washington was 28 m^3/ha (400 ft^3/acre) *(47)*. These are gross volume estimates. Because heart rot is prevalent in large yew trees, net volume would be considerably less.

In Idaho, analyses of increment cores and stem sections of yew trees from mature stands showed annual growth in diameter at 15 cm (6 in) above ground to range from 0.05 cm (0.02 in) to 0.25 cm (0.10 in). The following tabulation shows diameters by age class *(11)*:

Age in years	Diameter at 15 cm (6 in) above ground
25	2.5 cm (1.0 in)
50	5.0 cm (2.0 in)
75	11.4 cm (4.5 in)
100	15.2 cm (6.0 in)
125	22.9 cm (9.0 in)

The largest known Pacific yew tree is found in a cool, moist valley in western Washington *(28)*. Large yew trees are, however, more prevalent on somewhat drier sites with warm, moist winters. Forty-seven percent of all the yew trees larger than 30 cm (12 in) tallied on inventory plots on non-Federal land in California, Oregon, and Washington were in a 4-county area in southwestern Oregon at mid to low elevations in the drier interior valleys and slopes between the Cascade and Coast Ranges, and in the Klamath Mountains *(47)*.

Although Pacific yew is sometimes damaged by heat, frost, and wind, especially after overstory trees have been removed *(10,11,35,44)*, it can sometimes respond to release. On permanent plots in western Oregon measured 12 years apart, diameters of undamaged yew trees left after removal of overstory trees grew an average of 0.18 cm/yr (0.07 in/yr) and trees under dense overstories grew 0.06 cm (0.02 in) *(47)*.

The adaptation of Pacific yew to overstory removal is made possible through morphological changes in the needles—length, cuticle thickness, and deflection from the horizontal—and development of epicormic twigs *(10,11)*.

Rooting Habit—The root system of Pacific yew is deep and wide-spreading *(22)*.

Reaction to Competition—Pacific yew is very tolerant of shade *(1,11,44)*. It appears to require shade for establishment and can grow and develop under heavy forest canopies. On many sites, it is able to adapt to overstory removal (10,11), and large, old trees can be found that have been in the open much of their lives *(3)*.

Damaging Agents—Pacific yew is sensitive to damage from fire, and, where the overstory has been removed, it is sometimes damaged by exposure to the sun, wind, and cold *(10,11,26,35,44)*. It resists damage from sulfur dioxide and was the least sensitive of 12 coniferous species to smelter fumes at Trail, British Columbia *(26)*. Diseases of Pacific yew seedlings have not been studied, but *Rhizoctonia solani, Phytophthora cinnamoni,* and *Pythium sp.* have caused damping-off and seedling root rot in yews in the East. No serious leaf diseases have been reported. Snow blights—*Neopeckia coulteri* and *Herpotrichia juniperi*—have caused localized damage, and four needle blights are caused by *Macrophoma taxi, Mycosphaerella taxi, Phoma hystrella,* and *Sphaerulina taxi*. A stem canker is caused by *Diplodia taxi*, and twig blights by *P. hystrella* and *Physalopspora gregaria. Two root diseases—Armillaria ostoyae (obscura)* and *Phaeolus schweinitzii*—have been reported on Pacific yew in Idaho *(26)*.

Although seasoned heartwood of Pacific yew is extremely durable, large living Pacific yew trees often have heartrot or hollow boles *(11,23)*. Many of the yew trees over 50 cm (20 in) d.b.h. tallied on non-Federal land in California, Oregon, and Washington could not be bored to determine age because of rotten or hollow trunks *(47)*. Heartrot fungi infecting Pacific yew include *Phellinus nigrolimitatus, P. pini, P. robustus,* and *Fomitopsis rosea (26)*.

Several insects cause damage to yews in the eastern United States, including *Lecanium fletcheri* (called Fletcher scale or taxus lecanium), *Pseudococcus comstocki* (Comstock mealybug), *Dysmicoccus wistariae, Pseudococcus maritimus* (grape mealybug), and *Maladera castanea* (Asiatic garden beetle) *(2)*. No damage to Pacific yew in forested settings has been confirmed. Reported damage to Pacific yew foliage by budworms (*Choristoneura* spp.) in areas of heavy budworm infestation is thought to be heat or frost damage resulting from the defoliation of the overstory *(5,41)*.

Special Uses

The wood of Pacific yew has been used for archery bows, canoe paddles, tool handles, gunstocks, boat decking, furniture, musical instruments, carved figurines, and miscellaneous novelty items. (In a recent western State gubernatorial election, campaign buttons were made of yew wood.) Japanese have used Pacific yew for ceremonial "Toko" poles, which they place next to entrances of their homes *(6,19,23,29,44)*. Pacific yew's resistance to decay makes it useful for fenceposts. Of seven northwest species tested for use as untreated fenceposts, Pacific yew was the second most durable, with an average service life of 25 years *(33)*. In the mid-1980's Japanese purchasers paid $3,600 per thousand board feet (Scribner scale) for Pacific yew logs, mostly for wood carvings. In 1989, Japanese buyers agreed to pay $4,150 per thousand for grade 1 yew logs, and a Taiwanese buyer paid $6,100 *(7)*.

Among Native Americans, Saanich Tribal women used Pacific yew to remove underarm hair; Okanagans made a red paint from ground yew wood mixed with fish oil; several tribes smoked dried yew needles, which was said to cause dizziness; Haidas believed that women who ate yew berries would not conceive. Yew was valued as an item of trade and used in making instruments for hunting, fishing, and warring; tools, such as mauls and splitting wedges; household utensils, such as bowls and spoons; and medicine for a broad range of ailments *(23,29,44)*.

Pacific yew is again being used for medicinal purposes. In the late 1960's, taxol—a complex compound extracted from yew bark—was identified as a possible anticancer agent *(18,48)*. The National Cancer Institute (NCI) has found taxol to be one of the most promising of more than 120,000 plant compounds tested for anticancer properties. Taxol appears to be effective against a wide range of tumors, and good responses have been obtained in the treatment of refractory ovarian cancer *(9,38)*.

In 1988, the NCI acquired 27 700 kg (60,000 lb) of dried Pacific yew bark, collected from trees cut down in southwestern Oregon. On average, one yew tree yielded 18 kg (40 lb) of green bark, which weighed about 9 kg (19 lb) dried *(7)*. From the 27 700 kg of dried bark, about 4 kg (9 lb) of dry, crystalline taxol was extracted. Clinicians in several locations across the country have asked for increased supplies of taxol to expand tests to a broader range of cancer types. In January 1989, the NCI solicited another 27 700 kg of yew bark *(9)*.

The 27 700 kg of yew bark already collected and the second 27 700 kg ordered represent 6,000 to 7,000 trees. Most of these trees were cut or will be cut on Federal forest land where yew has not been inventoried. On non-Federal lands in California, Oregon, and Washington, where inventories have been made, there are an estimated 700,000 Pacific yew trees 28 cm (11 in) d.b.h. and larger, the size of most trees cut for bark collection. Almost all the yew trees on non-Federal land are survivors of logging operations that removed the old-growth overstory *(47)*. On Federal land where old-growth forests still exist, many more yew trees are thought to be present, but trees of the size needed to produce large quantities of bark are not abundant in most areas. An unknown but unquestionably significant percentage of the original yew resource has already been destroyed in logging. In the process of harvesting Douglas-fir and other timber species, mostly by clearcutting, yew trees were either cut or knocked over and broken up by machinery. Yew trees were seldom taken in primary logging operations, but some yew wood was later salvaged by firewood cutters and gleaners gathering wood for specialty products. Most of the yew trees that existed in logged areas were burned in slash-disposal fires. In many logged areas, the rootstocks have survived and resprouted, so, although the wood and bark of many yew trees were destroyed, there seems to have been little threat to the existence of the yew germ plasm.

Continued or increased demand for yew bark for taxol production could further decrease a resource that has already been greatly reduced. Attempts to synthesize taxol in the laboratory have failed, and prospects for success in the future are considered to be poor. The only known source of taxol now is yew bark. Taxol has been found in most of the several other species of *Taxus* that exist, but Pacific yew is the only one that is considered to be a practical source of quantities sufficient for clinical use *(9,12)*. At least one private organization has begun to investigate alternative ways of producing taxol, through tissue culture and by growing vegetatively propagated seedlings in a controlled environment *(7)*.

The several species of yew in both the western and eastern hemispheres are thought to have poisonous seeds and foliage. Incidents of livestock poisoning by yew have been reported in Europe and North America. Conversely, in both Europe and North America, domestic and wild animals are known to browse yew foliage without ill effects. If and under what conditions yew foliage is poisonous are not known *(13,14,22,32)*. Pacific yew is browsed by moose in the South Fork of the Clearwater River basin in Idaho, where the tree is considered critical to the animals' survival *(36)*. Pacific yew is also browsed heavily by elk and occasionally by deer in Oregon and Washington *(20,23,30)*.

Sprouts and epicormic branches that form in response to stand disturbance are favored by browsing animals. Repeatedly browsed yews in clearcut areas sometimes develop compact bushy crowns resembling the yew topiary of English gardens. Some limited use of *T. brevifolia* as an ornamental indicates it also has potential as a shade tree, for hedges, and for topiary *(23,44)*.

Genetics

Pacific yew occurs in nature as a shrub or a tree, but whether the two forms are distinct subspecies, races, or varieties is not known. Three cultivars have been reported: cv *erecta*, a columnar form; cv *nana*, a dwarf form; and cv *nutallii*, a drooping form. A hybrid between *Taxus brevifolia* and *T. cuspidata* (Japanese yew) has been reported, but has no botanical standing. Pacific yew was originally classified as a variety of *T. baccata* (European yew), which it closely resembles; some botanists grouped all seven of the currently recognized species of *Taxus* worldwide as varieties of *T. baccata*. Where different species grow near each other, interspecific hybrids frequently occur, lending support to the view that there is but one species *(13,22,23,34,44)*. Further evidence of the close similarity of the species of *Taxus* is provided by bark analyses which show that most species contain taxol *(9)*, and by an analysis of heartwood constituents of *T. baccata, T. brevifolia, T. cuspidata,* and *T. floridana*: the four species were found to be "chemically almost indistinguishable" *(15)*

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Thuja occidentalis L. Northern White-Cedar

Cupressaceae Cypress family

William F. Johnston

Northern white-cedar *(Thuja occidentalis)* is also called eastern white-cedar, arborvitae, and swamp-cedar. The name arborvitae or "tree of life" dates from the 16th century when the French explorer Cartier learned from the Indians how to use the tree's foliage to treat scurvy. A record tree in Michigan measures 175 cm (69 in) in d.b.h. and 34 m (113 ft) in height. The rot- and termite-resistant wood is used principally for products in contact with water and soil. The tree provides valuable shelter and browse in winter deeryards, and it is a widely planted ornamental.

Habitat

Native Range

The main range of northern white-cedar (fig. 1) extends through the southern part of the eastern half of Canada and the adjacent northern part of the United States. Specifically, it extends westward from Anticosti Island in the Gulf of St. Lawrence to the southern part of James Bay and through central Ontario to southeastern Manitoba; then south through central Minnesota and Wisconsin to a narrow fringe around the southern tip of Lake Michigan; then east through southern Michigan, southern New York, central Vermont and New Hampshire, and Maine. The species also grows locally in northwestern Ontario, west-central Manitoba, southeastern Minnesota, southern Wisconsin, north-central Illinois, Ohio, southern New England, and in the Appalachian Mountains from western Pennsylvania south to western North Carolina and eastern Tennessee.

Climate

Northern white-cedar grows in a relatively humid climate. Annual precipitation commonly ranges from 710 to 1170 mm (28 to 46 in), but the extremes range from about 510 mm (20 in) at the tree's northern and western limits to 1400 mm (55 in) in the southern Appalachians. One-third to one-half of the precipitation occurs during the warm season. Snowfall ranges from about 100 cm (40 in) to more than 380 cm (150 in) annually.

Temperatures are often cool during a moderately short growing season. The northern limit of the range extends to the forest-tundra transition (subarctic zone) in Canada. The southern limit has an average annual temperature of less than 10° C (50° F) in the Lake States and up to 16° C (60° F) in the southern Appalachians. Average January temperatures commonly range from –12° to –4° C (10° to 24° F) and those of July from 16° to 22° C (60° to 72° F). The average frost-free period commonly ranges from about 90 to 180 days, but the extremes range from less than 80 days at the tree's northern limit to about 200 days in the southern Appalachians *(16)*.

Soils and Topography

Northern white-cedar grows on a wide variety of organic soils (Histosols) and mineral soils (especially Inceptisols and Entisols); however, it does not develop well on extremely wet or extremely dry sites. It is most often associated with cool, moist, nutrient-rich sites, particularly on organic soils near streams or other drainageways, or on calcareous mineral soils. In Minnesota, however, white-cedar stands on uplands are primarily determined by an interaction of vegetation and lack of disturbance *(21)*. Northern white-cedar commonly grows on soils ranging from pH 5.5 to 7.2 *(9,36)*.

Northern white-cedar is usually dominant in rich swamps (forested rich fens) that have a strong flow of moderately mineral-rich soil water. The organic soil (peat) is usually moderately to well decomposed, 0.3 to 1.8 m (1 to 6 ft) thick, and often contains much rotted wood. It can also dominate the peat ridges in bog and fen complexes that have a sluggish movement of weakly enriched water *(22)*.

On mineral soil (upland) sites northern white-cedar is characteristic of seepage areas, limestone uplands, and old fields. It is common on shallow loam over broken limestone in southeastern Ontario and often forms pure stands in old fields and pastures on moist, well-drained soils in Maine *(9)*, southern Quebec, and southeastern Ontario. The tree also grows on calcareous clays, limestone cliffs, outcrops of acidic trap rock, and sandstone bluffs *(10,29)*.

Northern white-cedar generally grows best on limestone-derived soils that are neutral or slightly alkaline and moist but well drained. Nevertheless, most commercial stands are in swamps, where northern white-cedar can compete well with its associates *(13)* and is normally protected from fire *(23)*. Al-

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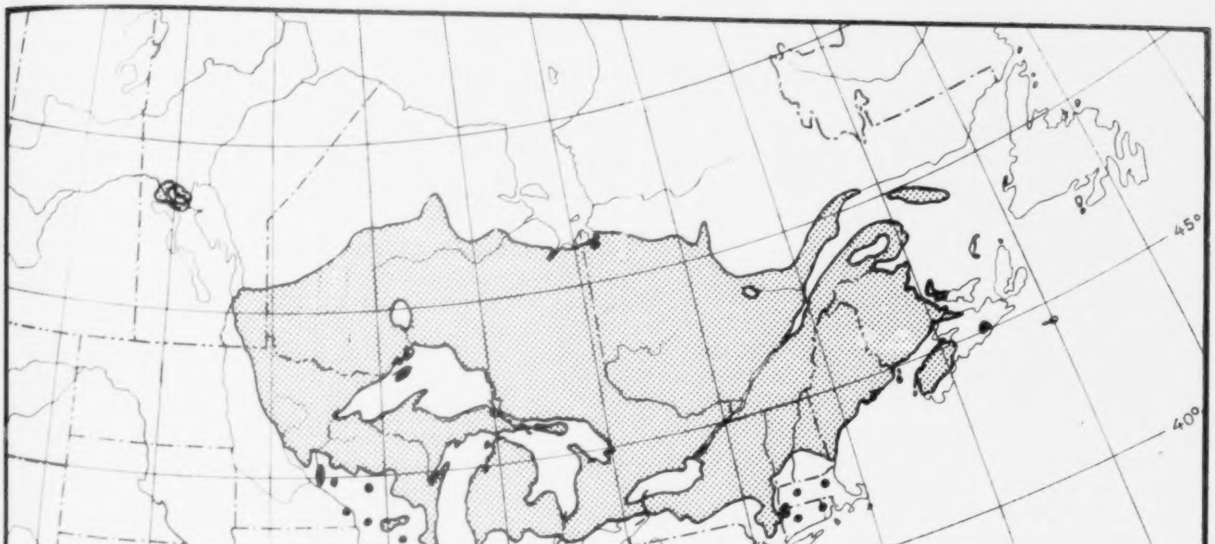
45°
40°
35°
30°
25°
20°
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
1984
100°
90°
80°
70°

Figure 1—*The native range of northern white-cedar.*

though old-field soils differ greatly, the tree's form and volume growth are much better on old fields than in poorly drained swamps *(9)*.

Northern white-cedar grows from near sea level to more than 600 m (2,000 ft), but within most of its range it is found between 150 and 600 m (500 and 2,000 ft).

Associated Forest Cover

Northern white-cedar most commonly grows in mixed stands but is also found in pure stands. It comprises a majority of the stocking or is pure in the Northern White-Cedar forest cover type (Society of American Foresters Type 37) and is an associate species in the following types *(13)*:

5	Balsam Fir
12	Black Spruce
13	Black Spruce–Tamarack
21	Eastern White Pine
23	Eastern Hemlock
24	Hemlock–Yellow Birch
30	Red Spruce–Yellow Birch
32	Red Spruce
33	Red Spruce–Balsam Fir
35	Paper Birch- Red Spruce–Balsam Fir
38	Tamarack
39	Black Ash–American Elm–Red Maple
108	Red Maple

The northern white-cedar type commonly includes some balsam fir *(Abies balsamea)* and tamarack *(Larix laricina)* in the boreal region of Canada but tends to be mixed with additional species farther south. Balsam fir, black spruce *(Picea mariana)*, white spruce *(P. glauca)*, red spruce *(P. rubens)*, tamarack, black ash *(Fraxinus nigra)*, and red maple *(Acer rubrum)* are common associates on the wetter sites, especially swamps. Yellow birch *(Betula alleghaniensis)*, paper birch *(B. papyrifera)*, quaking aspen *(Populus tremuloides)*, bigtooth aspen *(P. grandidentata)*, balsam poplar *(P. balsamifera)*, eastern hemlock *(Tsuga canadensis)*, and eastern white pine *(Pinus strobus)* are common on the better drained sites, especially uplands.

Except when dense, northern white-cedar stands usually have an undergrowth of shrubs and herbs. Speckled alder *(Alnus rugosa)* is commonly the most important shrub on the better sites. Other characteristic shrubs on the better sites (especially in swamps) include mountain maple *(Acer spicatum)*, red-osier dogwood *(Cornus stolonifera)*, and fly honeysuckle *(Lonicera canadensis)*. On poorer sites they include Labrador-tea *(Ledum groenlandicum)*, blueberries *(Vaccinium* spp.), and wintergreen (teaberry) *(Gaultheria procumbens)*; creeping snowberry *(G. hispidula)* is common on both kinds of sites (see *16* for a more complete list). Characteristic herbs on the better sites (especially in swamps) include dwarf raspberry *(Rubus pubescens)*, false lily-of-the-valley *(Maianthemum canadense)*, woodfern *(Dryopteris* spp.), and bunchberry *(Cornus canadensis)*. On poorer sites they include false Solomons-seal *(Smilacina trifolia)* and pitcherplant *(Sarracenia purpurea)*. Ground cover is usually a mosaic of sphagnum *(Sphagnum* spp.) and other mosses, liverworts, decaying logs, and litter *(13)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Male and female flowers of northern white-cedar, a monoecious species, are usually borne on separate twigs or branchlets; they are tiny, terminal, conelike bodies. Male flowers are yellowish and arise from branchlets near the base of the shoot; female flowers are pinkish and appear at the tips of short terminal branchlets. Ripe cones are pale cinnamon brown, oblong, and 8 to 13 mm (0.3 to 0.5 in) long.

In northeastern Minnesota, flower buds, which form during autumn, begin to expand the following spring from about mid-April to early May; pollen dispersal begins from late April to early June *(1)*. In northern Michigan flowering occurs from late April to early May, pollinated conelets begin to grow rapidly in late June, cones are full grown by mid-August, and cones ripen from August to September *(16,34,41)*. The period between cone ripening and cone opening is only from 7 to 10 days.

Seed Production and Dissemination—Cone production has been induced within 3 months of seed germination using gibberellic acid and a long photoperiod *(18)*. Under normal conditions cones have been found on northern white-cedars as young as 6 years old *(9)*. Seed production in large quantities begins when the trees are about 30 years old but is best after 75 years. An average-sized tree with a fairly full crown can produce about 9 liters (0.25 bu) of cones *(16)*, yielding 60,000 to 260,000 cleaned seeds. Limited data from Michigan indicate that white-cedar trees on upland sites produce more cones per tree, more seeds per cone, and a higher percentage of full seeds than those on swamp sites *(6)*.

Rangewide, northern white-cedar generally bears good or better seed crops at intervals of 2 to 5 years. However, during a 26-year period (1949–74) in northeastern Wisconsin, such crops were produced every 1 to 3 years, with medium crops to failures in the intervening years. In addition, it was found that good or better white-cedar seed crops can be predicted by similar-sized crops in red maple the preceding spring *(20)*.

Seed dispersal usually begins in September, although it sometimes begins as early as August. In the northern Lake States cones open from mid-September to late October *(1,41)*. Most of the seeds are released by November, but some seeds continue to fall throughout the winter.

Northern white-cedar seeds are light chestnut brown, about 6 mm (0.25 in) long, and have lateral wings about as wide as the body; cleaned seeds average 763,000/kg (346,000/lb) *(41)*. Most seed is wind disseminated, with the seeding range estimated to be from 45 to 60 m (150 to 200 ft) under normal conditions *(16)*.

Seedling Development—Northern white-cedar seeds remain viable for 5 years or more when stored in sealed containers at 6 to 8 percent moisture content and 0° to 3° C (32° to 38° F). As a rule the seeds have only slight internal dormancy. Under forest conditions dormancy is broken while the seeds lie on the ground during the first winter; thus fall sowing is generally recommended *(41)*. Because white-cedar seeds apparently do not remain viable in the forest floor longer than 1 year, such seeds should not be relied on for reproduction after clearcutting or fire *(6,17)*.

Germination is epigeal, with the cotyledons rising above the ground. The seed seems to germinate best at high temperatures such as 29° C (84° F) *(19)*, so that even though germination normally begins in May or June of the year following seed dispersal, it sometimes does not occur until late July or early August. Alternating day and night temperatures of 30° and 20° C (86° and 68° F), respectively, are recommended for germination tests *(41)*.

Northern white-cedar seeds germinate readily on a variety of moist substrates, but seedlings become established on only a few. The main requirements for early development seem to be a constant moisture supply and warm temperatures *(10,19)*. Although white-cedar generally grows best on neutral or slightly alkaline soil, seedlings do best on neutral or slightly acid soil but will grow on slightly alkaline soil *(16)*. On cutover white-cedar swamps in Minnesota, seedlings were found only where the pH of the surface soil (upper 10 cm or 4 in) ranged from 6.6 to 7.2 *(36)*.

On undisturbed areas, seedbeds of decaying (rotten) wood of logs and stumps account for more than 70 percent of the seedlings *(10,25)*. These seedbeds usually are more moist, warmer, and have less litter than other seedbed types *(19)*; they are also commonly dominated by mosses such as *Heterophyllium*, *Pleurozium*, and *Brotherella* *(25)*. Some seedlings become established—but usually much less frequently—on decayed litter, peat or humus, and sphagnum moss.

On disturbed areas, northern white-cedar seedlings commonly prosper on both upland and swamp burns. Broadcast burning (or wildfire) apparently must be fairly severe, however, to expose favorable, mineral soil seedbeds on uplands or to improve moss seedbeds in swamps *(27,48)*. White-cedar seedlings also reproduce well on skid roads where the compacted moss stays moist *(16)*. A heavy cover of slash hinders seedling establishment, but a light cover is more favorable than none *(27,48)*.

Northern white-cedar seedlings generally grow slowly under both forest and nursery conditions. Annual height growth averages only about 8 cm (3 in) during the first several years; seedlings can grow this much in 140 days under long photoperiods in growth chambers *(18)*. Stock raised in a nutrient solution and hardened in a nursery was superior to 3-year-old (2-1) nursery transplants *(49)*. In upland plantings transplants averaged 0.9 m (2.9 ft) tall at 9 years of age in the northern Lake States and 2.6 m (8.5 ft) tall at 12 years in Illinois *(26,29)*.

Although moisture is often the most important factor during the first few years, ample light is needed for continued seedling development. Seedlings were tallest when grown in about half of full light, but their shoots and roots were heaviest in full light *(31)*. In areas with frequent hot, dry spells, partial overstory shade is necessary to reduce losses from drought and herbaceous competition *(19)*.

Both shoot and radial growth generally begin in May and end by late August or in September in the northern Lake States and New Brunswick *(1,16)*.

Mortality of northern white-cedar seedlings during their early years is extremely high. Drought is probably the most important cause; seedlings on substrates such as thick moss, stumps, and hummocks often dry out during the summer. Other causes of early loss or damage include smothering by sphagnum moss or logging slash, cutting or girdling by small rodents such as the red-backed vole, and deer browsing (especially on planted stock) *(9,16,26,49)*.

Vegetative Reproduction—Northern white-cedar can send out roots from any part of a branch or stem if moisture conditions are favorable. Thus it frequently reproduces vegetatively in swamps, especially on poor sites with abundant sphagnum moss. If young seedlings are not considered, many more stems probably originate vegetatively than from seed in most swamps because vegetative reproduction is more tolerant of shade and is never without an adequate root system *(9)*.

Layering generally accounts for more than half the stems of white-cedar reproduction in northern Michigan and Maine swamps. It is most common in young stands and those with leaning trees, where the lower branches become covered by moss. Seedlings may produce layerings by age 5 or before *(16,34)*.

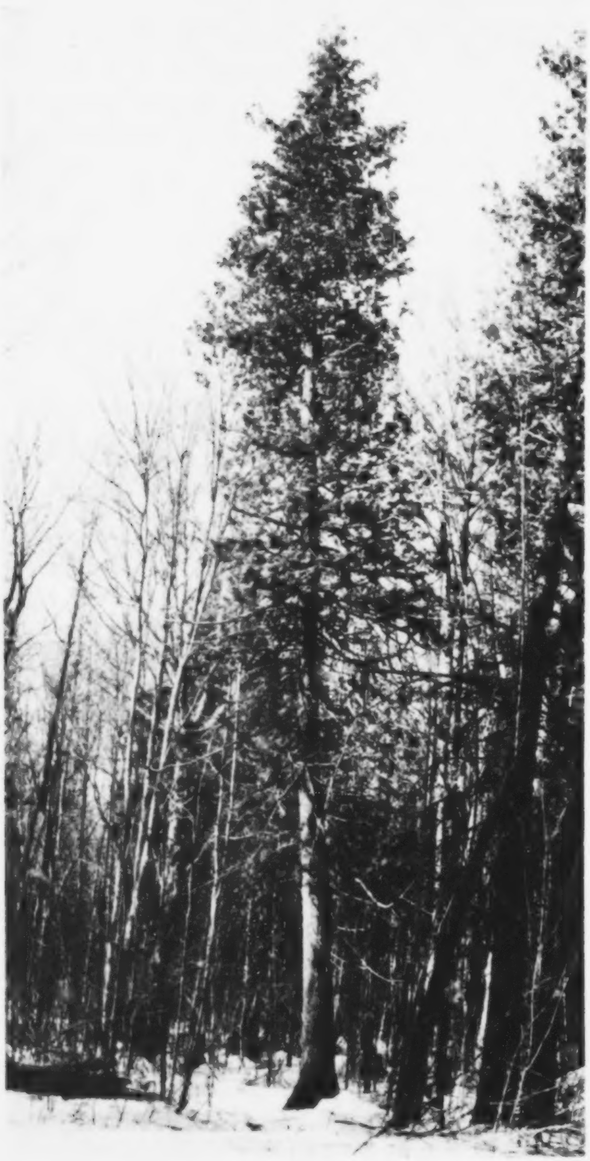

Figure 2—*A mature northern white-cedar on an upland site in northern Minnesota.*

New trees also develop vegetatively from uprooted trees whose vertical branches form roots. Sprouts from roots or stumps are generally rare *(16)*. Cuttings are commonly used to propagate cultivars of northern white-cedar; under forest conditions branchlets may be rooted by setting them out in deep sphagnum moss *(9)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Northern white-cedar is a medium-sized tree, commonly 12 to 15 m (40 to 50 ft) tall and 30 to 60 cm (12 to 24 in) in d.b.h. at maturity (fig.2). Infrequently it reaches 21 to 24 m (70 to 80 ft) tall and 120 to 150 cm (48 to 60 in) in d.b.h. *(10)*. Maximum dimensions reported are more than 30 m (100 ft) in height and 180 cm (72 in) in d.b.h. White-cedar reaches a maximum age of 400 years or more in swamps or on other lowland sites *(16)*.

The growth rate of northern white-cedar is greatly affected by site productivity and is expressed as site index or the height of dominants at age 50 years. In the Lake States, site index ranges from about 12 m (40 ft) on the best sites to 5 m (15 ft) on the poorest *(27)*. Indications are that the site productivity of white-cedar swamps could be increased substantially by drainage *(44)*. Northern white-cedar generally grows more slowly and attains less height than associated trees, especially in swamps.

Information on yield of northern white-cedar is limited mainly to normal yield tables for pure, fully stocked, even-aged stands in the Lake States (fig. 3). Such stands have yields at 120 years as shown in table 1 *(27)*.

Northern white-cedar reaches a maximum basal area of about 69 m²/ha (300 ft²/acre) *(8)*. Unfortunately for its value as timber, the tree commonly has a curved butt and poor form, especially in swamps *(9)*.

Little is known about biomass production, although components of various-sized white-cedars have been analyzed for weight (and nutrient elements) *(12)*. Above-ground biomass in one 70- to 100-year-old white-cedar stand totaled 159 t/ha (71 tons/acre) and had a net annual productivity of about 10 t/ha (4.5 tons/acre) *(38)*.

Timber rotations for northern white-cedar differ greatly with site productivity and management objective. Rotations for maximizing merchantable cubic volume range from 70 to 90 years for a site index of 12 m (40 ft) and from 80 to 100 years for an index of 9 m (30 ft). Rotations for sawtimber range from 110 to 140 years for a site index of 12 m (40 ft) and from 130 to 160 years for an index of 9 m (30 ft) *(27)*.

Table 1—Characteristics of fully stocked, even-aged stands of northern white-cedar in the Lake States *(27)*

Item	Site index at base age 50 years	
	9 m or 30 ft	12 m or 40 ft
Height of dominants and codominants, m	15	21
D.b.h., cm[1]	23	31
Trees/ha[1]	1112	618
Basal area, m^2/ha[1]	45	47
Merchantable volume, m^3/ha[2]	244	319
Sawtimber volume (Scribner), m^3/ha[3]	129	279
Height of dominants and codominants, ft	50	69
D.b.h., in[1]	8.9	12.4
Trees/acre[1]	450	250
Basal area, ft^2/acre[1]	195	205
Merchantable volume, ft^3/acre[2]	3,480	4,560
Sawtimber volume (Scribner) fbm/acre[3]	9,220	19,900

[1] Trees 0.25 cm (0.1 in) and larger in d.b.h.
[2] Peeled volume for trees 13 cm (5.0 in) and larger in d.b.h.
[3] Volume for trees 23 cm (9.0 in) and larger in d.b.h.

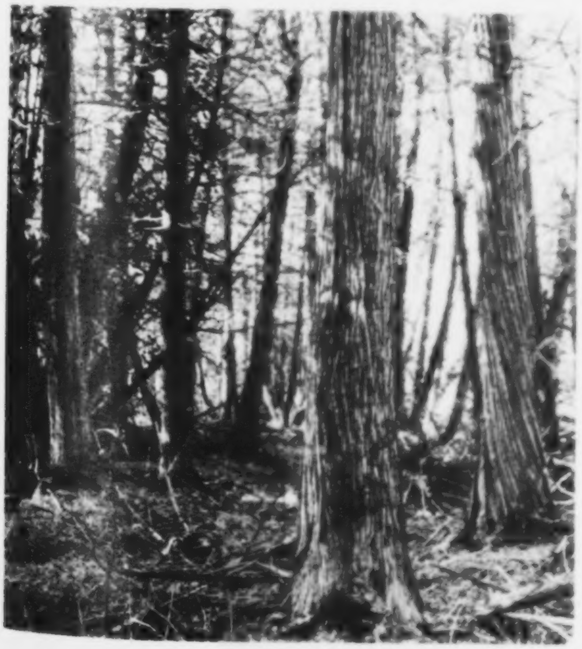

Figure 3—*A mature stand of northern white-cedar on a swamp site in northern Minnesota.*

Rooting Habit—Northern white-cedar seedlings grown in different soil media have shown that as moisture-holding capacity increases, root form changes from a long taproot with few laterals to shorter, thicker roots with many laterals. Root extension is particularly pronounced in rotten wood *(9)*. In Wisconsin, seedlings grown from seed collected in upland stands developed deep root systems in well-drained soils and shallow root systems in saturated soils; their lowland counterparts showed little plasticity in root development *(33)*.

After the seedling stage northern white-cedar generally develops a shallow, wide-spreading root system; and natural root grafts are fairly common. Because the tree grows on rocky cliffs throughout its range, the root system is apparently well adapted to secure water and nutrients from cracks in rocks *(10)*.

Reaction to Competition—Northern white-cedar is classed as shade tolerant, but it has been placed in three classes: very tolerant, tolerant, and intermediate. This variation probably exists because vegetative reproduction is considered more tolerant than seedlings *(9)*. Northern white-cedar is less tolerant than balsam fir but slightly more tolerant than black spruce. White-cedar can withstand severe suppression for several years, and it responds well to release not only during the reproduction period but at nearly all ages *(3,16)*.

Response to thinning northern white-cedar depends upon site quality, residual stand density, and stand age. In a well-drained Michigan swamp, a 45-year-old stand with a residual basal area of 15.8 m^2/ha (69 ft^2/acre) more than doubled its basal area in 8 years following thinning; a similar thinning in a poorly drained swamp showed no beneficial effect *(16)*. In a 65-year-old stand on a medium swamp site in Wisconsin, basal area growth following a second thinning was independent of stand density over a wide range. The growth rate decreased following the second thinning, however, probably because of increasing stand age *(14)*.

Both even-aged and uneven-aged stands of northern white-cedar are common. Even-aged stands develop in large swamp openings following wildfire or clearcutting *(13)*. In Wisconsin white-cedar often invades speckled alder thickets that form in swamps following wildfire or changes in water level; and it can reproduce directly on burned peat *(10)*. Even-aged stands also develop on abandoned upland fields in Maine (and southeastern Canada)—but apparently only where competition is not severe *(9)*.

Uneven-aged white-cedar stands are generally associated with the late stages of succession and are found mainly in swamps or on other moist sites *(23)*.

They develop where white-cedar reproduces in small openings created by partial cutting or wind damage, especially on poor sites where reproduction is mainly of vegetative origin. Uneven-aged stands also develop where white-cedar gradually succeeds associates—such as balsam poplar, tamarack, and black spruce—that are not as shade tolerant or long-lived *(13)*. However, understory white-cedars sometimes are not much younger than the overstory species; in such cases what appears to have developed through succession may really be due to suppression *(23)*.

Without major disturbance such as fire, the northern white-cedar type is exceedingly stable because the tree is long-lived and balsam fir is the only important associate sufficiently shade tolerant to grow in dense white-cedar stands *(10)*. Many stands, however, have been either opened by timber harvesting or severely browsed by white-tailed deer. In both cases, succession is often to balsam fir or swamp hardwoods, especially black ash *(27)*.

In Michigan's Upper Peninsula, northern white-cedar reproduction was most abundant after clearcutting in small blocks and narrow strips, and it should grow best after such cutting because hardwood competition is less than after partial cutting *(3)*. Shelterwood cutting is preferred, however, for the last blocks or strips to ensure adequate natural seeding *(27)*. This method of cutting also provides the partial overstory shade necessary to reproduce white-cedar in areas with frequent hot, dry spells *(19)*.

Successful deeryard management requires reproducing large, even-aged stands of white-cedar *(47)*. Because deeryard management and timber management are usually inseparable in the white-cedar type, the general recommendation is to produce large patches—16 to 65 ha (40 to 160 acres)—by harvesting small blocks annually *(48)*, using clearcutting or shelterwood cutting as indicated above. Satisfactory reestablishment of white-cedar after clearcutting, however, often requires some kind of site preparation, particularly broadcast burning of slash *(48)*. Where winter deer densities are high, the entire patch must be completely cleared in 10 years or less to minimize overbrowsing *(27)*; but where they are low, small blocks or narrow strips may be clearcut at 30-year intervals *(42)*.

Damaging Agents—On wet sites such as swamps, restricted soil aeration resulting from abnormally high water levels usually reduces the growth rate of northern white-cedar and may kill entire stands. Wetland road crossings and beaver damming are the primary causes of flooding. Road-caused flooding has killed white-cedar or reduced its growth on thousands of hectares in northern Minnesota *(45)*; natural gas and petroleum pipelines will probably have similar effects unless cross drainage is provided *(4)*.

Wind-induced uprooting and breakage sometimes occur in older stands on both upland and swamp sites, especially along exposed edges and in stands opened by partial cutting *(27)*. Large trees and those with basal defect are most susceptible to wind damage.

Northern white-cedar is highly susceptible to fire damage because its bark is thin and has a high oil content; its shallow roots are easily damaged even by light ground fires *(6)*. On the Laurentian Shield in northeastern Minnesota, this species has been driven to the lakeshores by fire *(23)*. The risk of wildfire is low, however, on most white-cedar areas in the United States and good fire protection now results in little loss *(27)*.

Snow and ice often damage northern white-cedar by breaking limbs *(6)*; they also break stems or force trees into a permanent leaning position *(7,9)*.

Agents that turn northern white-cedar foliage yellow or brown and sometimes cause severe damage or death include unfavorable winter weather, deicing salts, and drought. Plantings are particularly susceptible to winterkill caused by dehydration *(40)*. The tree's tolerance of deicing salts is only moderate or intermediate *(15,46)*; so branches exposed to salt spray along highways commonly have severe dieback. In Iowa windbreaks, white-cedar had more drought damage than other evergreens during a very dry winter *(37)*. When the oldest foliage turns rusty red in the fall, however, it is a natural shedding of branchlets (cladoptosis) *(39)*.

Northern white-cedar is relatively free from serious insect injury *(9,39)*. Carpenter ants and leafminers are probably its principal insect pests. The black carpenter ant *(Camponotus pennsylvanicus)* commonly reduces the timber value of large trees and often makes them subject to windbreakage. The red carpenter ant *(C. ferrugineus)* has caused significant damage in Minnesota *(2)*.

Leafminers are common pests of northern white-cedar. They have caused severe "scorching" of foliage and often subsequent twig, branch, or tree mortality in southeastern Canada *(39)*. Outbreaks of the arborvitae leafminer *(Argyresthia thuiella)* have severely damaged white-cedar stands in Maine, and damage to ornamentals and nursery seedlings is often severe. Ornamental white-cedars are also subject to serious injury by another leafminer, *Coleotechnites thujaella* *(2)*.

Several other insects and related organisms (such as mites) feed on northern white-cedar, but only a few are important. The bagworm *(Thyridopteryx ephemeraeformis)*, juniper scale *(Carulaspis juniperi)*, and spruce spider mite *(Oligonychus ununguis)* can significantly damage ornamental white-cedars *(39,50)*. Heavy infestations of the Fletcher scale *(Lecanium fletcheri)*, arborvitae aphid *(Cinara tujafilina)*, and arborvitae weevil *(Phyllobius intrusus)* have occurred in nurseries *(2)*.

Northern white-cedar has few serious diseases as a forest tree, especially in immature stands; whereas in cultivation it is subject to several seedling and foliage diseases. Seedlings seem to be resistant to damping-off fungi, however. The foliage-blight fungi *Phomopsis juniperovora* and *Didymascella thujina* are among the main organisms causing seedling diseases. Beyond the seedling stage *Phomopsis juniperovora* blights foliage and shoots under humid conditions, and *Didymascella thujina* causes some unsightliness. In Quebec a snow-blight fungus *(Phacidium* sp.) has caused important damage in nurseries and hedges *(24)*.

Although several root- and butt-rot fungi attack northern white-cedar, they mainly attack old or damaged trees. Because fruiting bodies of these fungi seldom appear on living trees, the most common outward sign of rot is woodpecker holes. *Poria subacida*, causing a white stringy butt rot, and balsam (or brown) butt rot *(Tyromyces balsameus)* and red-brown butt rot *(Phaeolus schweinitzii)*, both causing cubical rots, are common in trees on knolls or other drier parts of swamps *(16)*. Balsam butt rot can also cause extensive root rot in suppressed white-cedars *(24)*.

Winter browsing by white-tailed deer often severely damages older seedling- and sapling-stage northern white-cedar in the Lake States and can prevent the satisfactory reestablishment of the type after harvesting *(27)*, especially in deeryards. In some areas, however, damage from snowshoe hares is as great as, or greater than, from deer *(16)*.

Porcupines sometimes kill white-cedar trees or lower their growth and timber quality by feeding heavily on foliage and by girdling stems and branches. Red squirrels frequently clip branchlets with flower buds and cone clusters, and thus may significantly reduce the supply of seed available for reproduction *(6)*. Both porcupine and squirrel damage contribute to the prevalence of stag-headedness in old trees *(9)*.

Special Uses

The principal commercial uses of northern white-cedar are for rustic fencing and posts; other important products include cabin logs, lumber, poles, and shingles. Smaller amounts are used for paneling, piling, lagging, pails, potato barrels, tubs, ties, boats (especially canoes), tanks, novelties, and woodenware *(28)*. Recently, white-cedar has been used for making kraft pulp and it appears excellent for particleboard. "Cedar leaf oil" is distilled from boughs and used in medicines and perfumes; boughs are also used in floral arrangements *(32)*.

The northern white-cedar type is valuable for wildlife habitat, particularly for deeryards during severe winters. The tree is highly preferred by white-tailed deer for both shelter and browse. Sapling stands produce a great amount of deer food *(47)* and clearcut stands in Michigan yielded almost 6000 kg/ha (5,340 lb/acre) of browse from tops *(16)*. White-cedar is also utilized by such mammals as the snowshoe hare, porcupine, and red squirrel. Its browse is generally rated as highly preferred by hares *(5,30)* and is sometimes heavily utilized *(6)*. Birds common in white-cedar stands during the summer include several warblers (northern parula, black-throated green, blackburnian, black-and-white, and magnolia), white-throated sparrows, and kinglets *(9,11)*. The pileated woodpecker commonly excavates cavities in mature white-cedars to feed upon carpenter ants.

Northern white-cedar forms an attractive fringe around some lakes and peatlands. Stands with high basal area, large trees, and little undergrowth are especially attractive *(35)*. The tree's unusual bark and foliage patterns are esthetically appealing to many forest users *(27)*.

Northern white-cedar is widely used for ornamental plantings in the United States *(24)*, is now common in Newfoundland, and has been grown in Europe since the 16th century. White-cedar is particularly useful for barrier and shelter plantings *(29)*, and it is one of the few conifers recommended for power line rights-of-way *(43)*.

Northern white-cedar has limited value as a watershed protector because it usually grows on gently sloping terrain. Although harvesting of white-cedar is presently on a small scale, clearcutting on peatland sites has little effect on annual water yields or water tables. Nutrient concentrations in streamflow or temperatures in trout streams should not increase significantly unless harvesting is on a massive scale *(27,35)*.

Genetics

Population Differences and Races

Northern white-cedar is morphologically similar throughout its range, with no races or varieties reported. But a rangewide provenance study indicates that significant genetic variation does exist.

In the Lake States, provenances from intermediate latitudes generally grew best *(26)*; in Illinois, provenances from south of the species' main range were shortest but a definite geographic pattern was lacking, perhaps because of localized ecotypes *(29)*. In Wisconsin, upland and lowland populations less than 0.7 km (0.4 mi) apart may form separate ecotypes *(33)*, but the extent of differentiation seems to vary from one area to another.

The existence of more than 120 ornamental cultivars of northern white-cedar, which differ in foliage color and growth habit, also reflects significant genetic variation in natural populations.

Hybrids

No natural or artificial hybrids have been reported *(6,33)*.

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Thuja plicata Donn ex D. Don Western Redcedar

Cupressaceae Cypress family

Don Minore

Western redcedar *(Thuja plicata)*, also called Pacific redcedar, giant-cedar, arborvitae, canoe-cedar, and shinglewood, is the only *Thuja* species native to western North America. Extant redcedar volumes are estimated to be 824 million m^3 (29 billion ft^3) in British Columbia *(43)* and 228 million m^3 (8 billion ft^3) in the United States *(16)*. Most of this volume is in mature trees, which have tapered, often-fluted bases, drooping branches, thin fibrous bark, and small scalelike leaves arrayed in flat sprays. Many have forked tops (fig. 1). They often reach ages of 800 to 1,000 years. One particularly large specimen in Washington has a d.b.h. of 592 cm (233 in), a height of 54.3 m (178 ft), and a crown spread of 16.5 m (54 ft). The wood is valuable and extensively used in a wide variety of products.

Habitat

Native Range

Western redcedar grows along the Pacific coast from Humboldt County, CA (lat. 40° 10′ N.), to the northern and western shores of Sumner Strait in southeastern Alaska (lat. 56° 30′ N.) (fig. 2). In California, it is common only in the lower Mad River drainage and the wet region south of Ferndale in Humboldt County; it is found elsewhere only in isolated stands in boggy habitats *(19)*. North of the California–Oregon border, the coastal range broadens to include the western slopes of the Cascade Range north of Crater Lake and the eastern slopes north of about latitude 44° 30′ N. *(12)*. Optimal growth and development of western redcedar are achieved near the latitudinal center of its range—Washington's Olympic Peninsula.

North of the Olympic Peninsula and Vancouver Island, the coastal range narrows again and is restricted to the Coast Ranges and offshore islands. A few scattered stands are found between the Coast Ranges and the Selkirk Mountains near the southern border of British Columbia, but redcedar's coastal range is essentially isolated from its interior range.

The interior range extends south from the western slope of the Continental Divide at latitude 54° 30′ N. in British Columbia through the Selkirk Mountains into western Montana and northern Idaho *(2)*. The southern limit is in Ravalli County, MT (lat. 45° 50′ N.). With the possible exception of a few trees east of the Continental Divide near the upper end of St. Mary Lake, Glacier County, the eastern limit of the

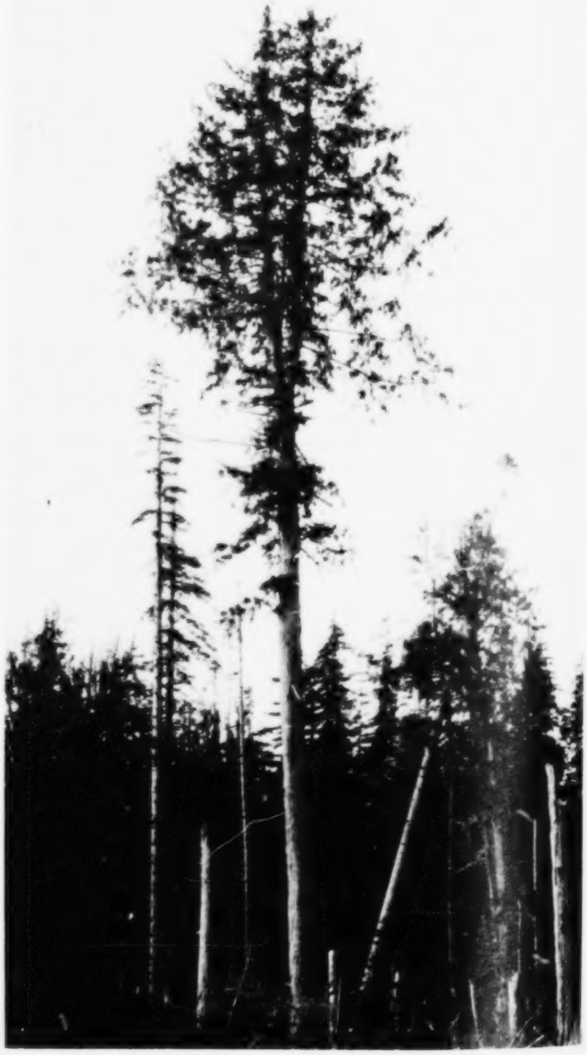

Figure 1—*Mature western redcedar with forked top (Courtesy of Edmond C. Packee, Macmillan Bloedel Ltd.)*

The author is Principal Plant Ecologist, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

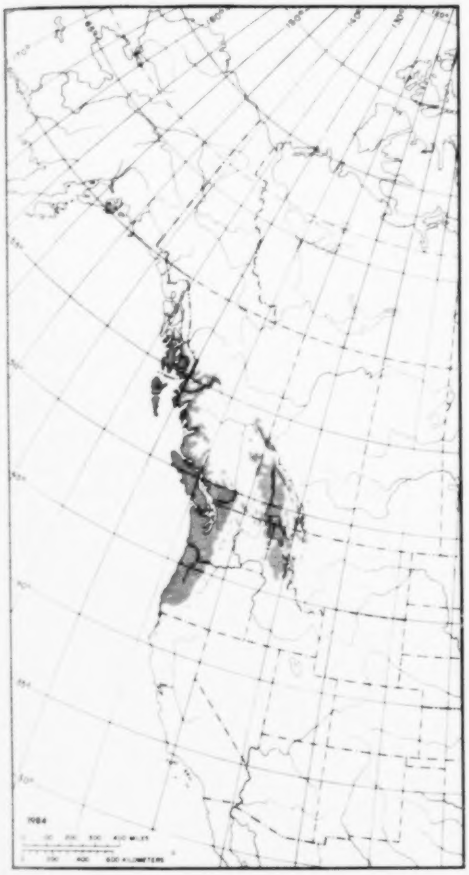

Figure 2—*The native range of western redcedar.*

range of redcedar is near Lake McDonald in Glacier National Park, MT.

Climate

Coastal western redcedar receives from less than 890 mm (35 in) of annual precipitation to more than 6600 mm (260 in), mostly as winter rainfall; interior western redcedar, about 710 mm (28 in) in the north, 810 to 1240 mm (32 to 49 in) farther south—about half as spring and autumn rain, one-third as winter snow *(2)*.

Although western redcedar is abundant in many forested swamps, it is sometimes found on sites that are too dry for western hemlock *(Tsuga heterophylla) (12,39,42)*, probably because the root penetration of the redcedar is better. Redcedar leaves are not protected from excessive transpiration by cutin and wax.

Trees tolerate stagnant winter water tables averaging less than 15 cm (6 in) below the soil surface on the Olympic Peninsula *(32)*. The species dominates wet ravines and poorly drained depressions in both Glacier National Park in Montana and the Selway Bitterroot Wilderness in Idaho *(20,21)*.

Where sufficient precipitation is present, low temperature appears to limit the species' range. Length of the frost-free period abruptly decreases just above the tree's upper elevation limits on Vancouver Island. The northern limits of western redcedar lie between the 11.1° and 11.7° C (52° and 53° F) mean summer temperature isotherms in southeastern Alaska. Absolute minimum temperatures experienced by western redcedar in British Columbia are -10° to -30° C (14° to -22° F) in coastal populations, -14° to -47° C (7° to -53° F) in the interior *(28)*. Western redcedar has a growing season of at least 120 frost-free days along the coast but as few as 75 frost-free days in some portions of its interior range. It is not resistant to frost and is sometimes damaged by freezing temperatures in late spring or early autumn.

Soils and Topography

Western redcedar can tolerate a wide range of soil properties in most localities. Soils on which it is most commonly found are in the orders Inceptisols, Ultisols, and Histosols. It is found on all landforms, soil textures, and parent materials on Vancouver Island *(39)*. In southwestern Oregon, it grows on sedimentary, metasedimentary, gabbroic, dioritic, granodioritic, and occasionally even serpentinite and peridotite parent materials *(24)*. Coarse sandy soils are not well suited to establishment and growth of redcedar in northern Idaho and northeastern Washington, but rocky slopes with limited soil development support redcedars in southeastern Alaska. Poorly drained organic soils also support redcedar south of Petersburg, AK. It grows on loams, clays, sands, chalk downland, and *Molina–Juncus* peat in England, but is most competitive on fine-textured lowland soils there. It grows well on shallow soils over chalk and can tolerate both acid and alkaline soil conditions *(45)*.

Western redcedar seems able to survive and grow on soils that are low in nutrients and is found on such soils over much of its natural range. Site index is positively correlated with foliar nitrogen, sulfur, copper, boron, and chlorophyll. However, productivity may be improved by fertilization *(44)*. When grown in well watered soil fertilized with nitrogen, phosphorus, and potassium, redcedar seedlings outgrow the seedlings of Douglas-fir *(Pseudotsuga menziesii)*, grand fir *(Abies grandis)*, Sitka spruce *(Picea sitchensis)*, western hemlock, and ponderosa pine *(Pinus ponderosa)*. Available nitrogen, calcium, and water appear to be the most important factors affecting growth and establishment of redcedar. Established redcedars tend to raise soil cation exchange capacities, pH's, and amounts of exchangeable calcium *(1)* and thus benefit the soils in which they grow.

Western redcedar grows from sea level to 910 m (3,000 ft) in southeastern Alaska. In British Columbia, the elevational range is higher—from sea level to 1190 m (3,900 ft). Redcedar is found in the interior (fig. 3) from 320 m (1,050 ft) to 2130 m (7,000 ft). The greatest range in elevation occurs in Oregon, where the species occurs from sea level to 2290 m (7,500 ft) at the rim of Crater Lake.

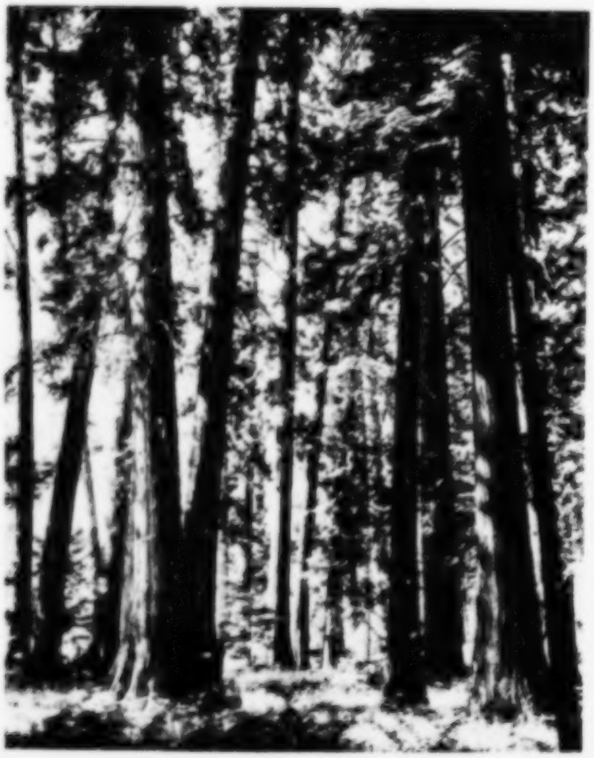

Figure 3—*A virgin stand of western redcedar in a Kaniksu National Forest natural area in Idaho.*

Associated Forest Cover

Pure stands of western redcedar cover some small areas, but it is usually associated with other tree species. Along the coast these include black cottonwood *(Populus trichocarpa)*, bigleaf maple *(Acer macrophyllum)*, western hemlock, mountain hemlock *(Tsuga mertensiana)*, Sitka spruce, western white pine *(Pinus monticola)*, lodgepole (shore) pine *(P. contorta)*, Port-Orford-cedar *(Chamaecyparis lawsoniana)*, Alaska-cedar *(C. nootkatensis)*, incense-cedar *(Libocedrus decurrens)*, Douglas-fir, grand fir, Pacific silver fir *(Abies amabilis)*, red alder *(Alnus rubra)*, Pacific madrone *(Arbutus menziesii)*, and Pacific yew *(Taxus brevifolia)*. Several of these species (black cottonwood, western hemlock, western white pine, Douglas-fir, grand fir, and Pacific yew) are also associated with western redcedar in the interior. Subalpine fir *(Abies lasiocarpa)*, western larch *(Larix occidentalis)*, Engelmann spruce *(Picea engelmannii)*, white spruce *(P. glauca)*, lodgepole pine, and ponderosa pine are also associated with redcedar in the interior.

Redcedar is a major component of two forest cover types *(11)*: Western Redcedar (Society of American Foresters Type 228) and Western Redcedar–Western Hemlock (Type 227). It is a minor component of the following types:

210	Interior Douglas-Fir
212	Western Larch
213	Grand Fir
215	Western White Pine
218	Lodgepole Pine
221	Red Alder
222	Black Cottonwood–Willow
223	Sitka Spruce
224	Western Hemlock
225	Western Hemlock–Sitka Spruce
226	Coastal True Fir
229	Pacific Douglas-Fir
230	Douglas-Fir–Western Hemlock
231	Port-Orford-Cedar
232	Redwood

Some associated shrub species are listed in table 1. Several occur in both interior and coastal environments, but Rocky Mountain honeysuckle *(Lonicera utahensis)* and clematis *(Clematis columbiana)* are associated with redcedar only in the interior, whereas salmonberry *(Rubus spectabilis)* and red huckleberry *(Vaccinium parvifolium)* are found only on the Pacific slope. Pacific rhododendron *(Rhododendron macrophyllum)* is an abundant associate in coastal California, Oregon, and

Table 1—Shrub species often associated with western redcedar in coastal and interior portions of its native range.

Coastal	Interior	Both Coastal and Interior
Oregongrape *(Berberis nervosa)*	Mountain alder *(Alnus tenuifolia)*	Western serviceberry *(Amelanchier alnifolia)*
Stink currant *(Ribes bracteosum)*	Creeping western barberry *(Berberis repens)*	Rustyleaf menziesia *(Menziesia ferruginea)*
Alaska blueberry *(Vaccinium alaskaense)*	Common juniper *(Juniperus communis)*	Thimbleberry *(Rubus parviflorus)*
Box blueberry *(Vaccinium ovatum)*	Cascade azalea *(Rhododendron albiflorum)*	Oceanspray *(Holodiscus discolor)*
Red huckleberry *(Vaccinium parvifolium)*	Red raspberry *(Rubus idaeus)*	Devilsclub *(Oplopanax horridum)*
Salmonberry *(Rubus spectabilis)*	Blue huckleberry *(Vaccinium globulare)*	Pachistima *(Pachistima myrsinites)*
Pacific rhododendron *(Rhododendron macrophyllum)*	Rocky Mountain honeysuckle *(Lonicera utahensis)*	Baldhip rose *(Rosa gymnocarpa)*
Salal *(Gaultheria shallon)*	Clematis *(Clematis columbiana)*	Common snowberry *(Symphoricarpos albus)*
		Ovalleaf huckleberry *(Vaccinium ovalifolium)*

Washington, but it is rare and confined to isolated locations in south-coastal British Columbia. Salal *(Gaultheria shallon)* also is an abundant associate. Its range extends farther south than that of redcedar, but the northern limits of salal are nearly the same as the northern limits of western redcedar in coastal Alaska.

Some associated herb species are listed in table 2. Many are common in both coastal and interior environments. However, slough sedge *(Carex obnupta)*

Table 2—Herb species often associated with western redcedar in coastal and interior portions of its native range.

Coastal	Interior	Both Coastal and Interior
Threeleaf anemone *(Anemone deltoidea)*	Goldthread *(Coptis occidentalis)*	Maidenhair fern *(Adiantum pedatum)*
Deerfern *(Blechnum spicant)*	Everlasting corydalis *(Corydalis sempervirens)*	Ladyfern *(Athyrium filix-femina)*
Slough sedge *(Carex obnupta)*	Malefern *(Dryopteris filix-mas)*	Western swordfern *(Polystichum munitum)*
Pacific water-parsley *(Oenanthe sarmentosa)*	Largeleaf avens *(Geum macrophyllum)*	Mountain woodfern *(Dryopteris austriaca)*
Oregon oxalis *(Oxalis oregana)*	Roundleaf alumroot *(Heuchera cylindrica)*	Prince's-pine *(Chimaphila umbellata)*
Dwarf blackberry *(Rubus lasiococcus)*	Panicle bluebells *(Mertensia paniculata)*	Bunchberry *(Cornus canadensis)*
Youth-on-age *(Tolmiea menziesii)*	Pine drops *(Pterospora andromedea)*	Skunkcabbage *(Lysichitum americanum)*
White inside-out flower *(Vancouveria hexandra)*	Green pyrola *(Pyrola chlorantha)*	False Solomon's-seal *(Smilacina stellata)*
Evergreen violet *(Viola sempervirens)*		Pacific trillium *(Trillium ovatum)*

and Pacific water-parsley (*Oenanthe sarmentosa*) are limited to moist habitats west of the Cascades, whereas wild sarsaparilla (*Aralia nudicaulis*) and goldthread (*Coptis occidentalis*) occur with redcedar only in the interior.

Coastal redcedar plant communities in British Columbia have been classified into 24 associations under 9 alliances in the *Thuja–Rubus spectabilis* order (*35*). Communities listed in less detailed coastal classifications include redcedar/swordfern, redcedar/devilsclub/maidenhair fern, redcedar/maidenhair fern-ladyfern, redcedar–western hemlock/devilsclub/ladyfern, redcedar–grand fir/mountain boxwood, redcedar–grand fir/swordfern, redcedar–Douglas-fir/Oregongrape, redcedar–Sitka spruce–red alder/skunkcabbage-slough sedge, and redcedar/skunkcabbage (*12,28*).

The redcedar/skunkcabbage plant community also occurs in the interior; where redcedar/devilsclub, redcedar/devilsclub/coolwort (*Tiarella trifoliata*), redcedar/queenscup (*Clintonia uniflora*), and redcedar/maidenhair fern are found (*7,28,42*).

Life History

Reproduction and Early Growth

Flowering and Fruiting—When grown in the open, western redcedars begin to produce strobili at 10 years of age and usually every other year thereafter. Strobilus development can be artificially induced at younger ages and increased in mature trees by girdling or treating with gibberellin (*8*). The species is monoecious; male and female strobili are produced on different branches of the same tree, at different heights—the reddish male strobili on lower branches and the green female strobili nearer the treetops and farther from the trunk (*38,52*). Anthesis and pollination occur during March and April in southern stands near the coast. They occur during May and June in coastal Alaska and interior stands (*47*).

Seed Production and Dissemination—Each mature strobilus usually produces only 3 to 6 seeds (*8*), but the strobili are often numerous and heavy seed crops are common. In dry years, conebearing stands in the interior tend to be on high, moist sites (*14*). Average annual seed crops vary from 247,000 to 2,470,000 seeds per hectare (100,000 to 1 million/acre) in coastal forests and from 54,000 to 274,000/ha (22,000 to 111,000/acre) in the interior. Major seedfall occurs during October and November in both ranges (*2*). Gibberellin-treated, containerized seed orchards should permit efficient management of seed production and harvesting (*8*).

Seeds are small—448,000 to 1,305,000/kg (203,000 to 592,000/lb) (*47*). They fall faster and do not fly as far as the seeds of western hemlock, Sitka spruce, and Douglas-fir, but dissemination is adequate within 100 m (330 ft) of a seed source (*4,30*). The seeds usually germinate well without stratification, and they retain their initial viability for at least 7 years when stored dry (5 to 8 percent moisture) at –18° C (0° F) (8). Germination is epigeal.

Seedling Development—Most seeds escape rodent and bird predation, but seedling mortality is high during the germination period (*15*). Where moisture and temperature conditions are favorable, germination can occur in the autumn, winter, or spring. Almost no germination occurs after the first year, however. Seedbed quality may be critical.

Throughout the range of western redcedar, disturbed mineral soil seedbeds seem to be a major requirement for regeneration from seed (*41*). Although unburned soil benefits redcedar more than soil that has been scorched, slash burning favors redcedar by creating more mineral soil surfaces in cutover areas. Rotten wood that is in contact with the soil is the preferred seedbed in old redcedar groves (*41*). Partial shade is beneficial because drought and high soil temperature damage seedlings in full sunlight, and poor root penetration causes damage from drought in full shade (*48*).

Direct seeding in the autumn is successful where soil moisture is available, but large quantities of seed may be required to obtain adequate stocking. In the nursery, spring sowing is best; half-shaded seedbeds are recommended (*47*). Pelleting the seeds makes them more compatible with automated nursery sowing machinery (*8*). Containerized nursery seedlings can be produced in 7 months. They survive as well or better than bare-root stock when planted in coastal Oregon, Washington, and British Columbia, but 2-year-old bare-root stock tends to be most cost effective in the coastal range (*6*). When bare-root stock is planted, recently lifted dormant seedlings with low shoot/root ratios should be used and cold storage avoided whenever possible. Containerized stock planted in the spring appears to perform better than bare-root stock in the interior (*18*). Natural regeneration is important in the northern Rocky Mountains, where it is most frequently successful on westerly and northerly aspects in western redcedar habitat types (*18*).

Western redcedar seedlings are less tolerant of high soil temperature and of frost than are the seedlings of Engelmann spruce, grand fir, and Douglas-fir. The exposed upper foliage of young redcedars often sunburns severely *(31)*. Roots of seedlings grow more slowly than the roots of Douglas-fir and incense-cedar, but they outgrow the roots of seedling western hemlock and Sitka spruce. Shoots have a longer growth period than any associated conifer. Nonrigid leaders are produced, and neither lateral nor terminal shoots form dormant buds. Lateral shoot growth is vigorous, amounting to at least 80 percent of terminal shoot growth in young redcedars *(31)*. Seedlings account for most of the western redcedar regeneration in clearcuts and other disturbed areas. On good coastal sites, they grow as tall or taller than Douglas-fir, western hemlock, and Sitka spruce seedlings during the first 5 years *(6,51)*. The redcedars are subsequently overtaken by Douglas-firs (by age 10) and western hemlocks (by age 15).

Vegetative Reproduction—Three types of natural vegetative reproduction occur: layering, rooting of fallen branches, and branch development on fallen trees. The resulting "veglings" are more abundant than seedlings in mature Idaho stands *(40)*. Saplings that have been knocked down in the western Cascades often regenerate when their branches root.

Redcedar clones are easily propagated by the rooting of stem cuttings. Although untreated cuttings will root, a 1-minute dip in a 3,000 ppm solution or a 4-hour soak in a 200 to 400 ppm solution of indolebutyric acid improves rooting speed, the number of cuttings rooted, and the total length of roots per cutting. Ramets for seed orchards can be produced by treating cuttings with indolebutyric acid, then rooting them in a 1-to-1 mixture of peat and perlite *(8)*. Young fragmented stems can be induced to bud after being soaked in a cytokinin solution, and the resulting buds can be rooted on a culture medium that contains napthalineacetic acid and kinetin *(33)*.

Sapling and Pole Stages to Maturity

Growth and Yield—Intermediate redcedars are distinguishable from dominants by age 5 on good sites. Codominants usually can be differentiated from dominants by age 25 (fig. 4). Mean annual height growth of the dominants is 0.5 m (1.64 ft) in 40- to 60-year-old, pure, second-growth stands on moist sites in western Washington *(36)*. Annual radial increments of 10 mm or even 20 mm (0.4 to 0.8 in) occur on the best moist sites in the south coast region of British Columbia *(39)*.

Pure, even-aged stands can attain volumes comparable to pure Douglas-fir stands by age 50 on high-quality upland sites in western Washington *(37)*. Plantations should be dense (about 2,470 trees per hectare or 1,000/acre), and intermediate crown classes should be removed in a light thinning to reduce side shade at about age 25 *(22,36)*. Stands of 370 to 430 crop trees/ha (150 to 175 crop trees/acre) at time of harvest may allow maximum diameter growth without causing poor form *(36)*. Maintaining a nearly closed canopy at all times will benefit form because open-grown redcedars tend to develop excessively large limbs and multiple tops. Faster growing trees of acceptable quality can be grown at wide spacings if their lower boles are pruned *(50)*, but percentages of latewood decrease significantly *(49)*.

Volumes of 379 to 825 m^3/ha (5,418 to 11,782 ft^3/acre) were measured in 40- to 60-year-old pure second-growth stands on moist sites in western Washington *(36)*. A yield model on medium sites in British Columbia indicates yields of 70 m^3/ha (1,000 ft^3/acre) at age 40, 350 m^3/ha (5,000 ft^3/acre) at age 115, and 595 m^3/ha (8,500 ft^3/acre) at age 270; maximum current annual increment occurs at 82 years and maximum mean annual increment at 130 years *(34)*.

In Great Britain, the cumulative volume produced by normal western redcedar stands on poor sites is 50 m^3/ha (714 ft^3/acre) at age 20 and 953 m^3/ha (13,620 ft^3/acre) at age 80. On good sites, cumulative volume produced is 232 m^3/ha (3,315 ft^3/acre) at age 20 and 1839 m^3/ha (26,268 ft^3/acre) at age 80. The average age of maximum mean annual increment is 72 on poor sites and 58 on good sites in these British stands *(22)*. At ages 20 and 50, cumulative volume production is lower for western redcedar than for Douglas-fir and Sitka spruce in Great Britain, but by age 80 the redcedar volume production is higher than that of Douglas-fir and spruce *(45)*.

Growth is often much slower. Suppressed redcedar trees that are 200 years old but only 7.6 cm (3 in) in d.b.h. and 7.6 m (25 ft) tall are not unusual. Survival for such long periods of suppression may be due to the ability of the species to produce new root growth in full shade. It may also be a result of frequent root grafting. Dominant trees often support growth of the root systems and lower boles of suppressed trees *(9)*.

Rooting Habit—Tree roots are extensive. Redcedars made up only 17 percent of the basal area but accounted for 82 percent of the root length in a mixed-species stand in northern Idaho *(29)*. Tap roots are poorly defined or nonexistent, but fine roots develop a profuse, dense network.

Western redcedar roots usually are deeper than the roots of western hemlock but shallower than the roots of western larch, western white pine, grand fir, and Douglas-fir *(30)*. The soils on which these species

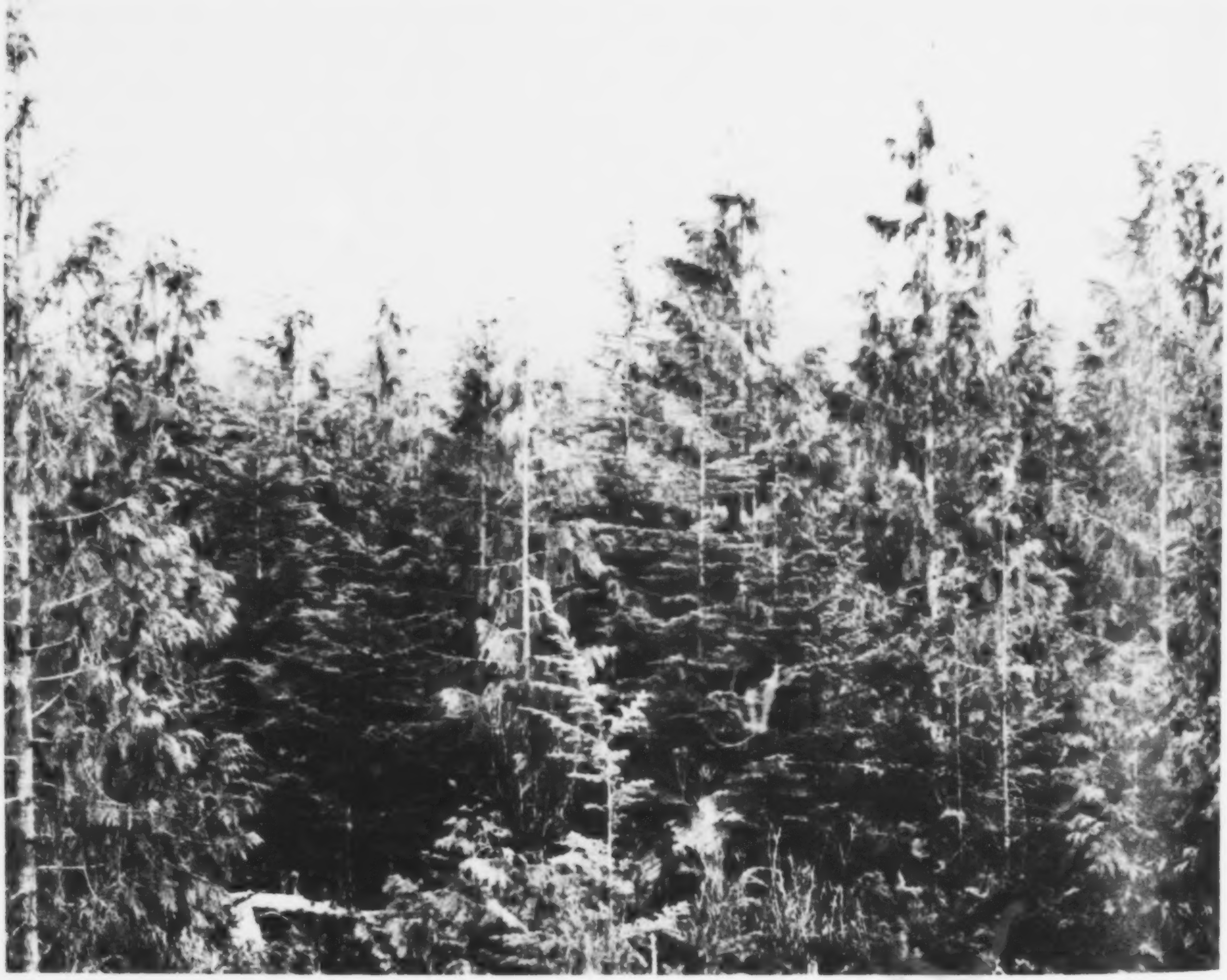

Figure 4—*A 25- to 30-year-old stand of western redcedar on Vancouver Island, BC, showing early crown-class differentiation. (Courtesy of Edmond C. Packee, Macmillan Bloedel Ltd.)*

usually grow may be responsible, however, because western redcedar, western hemlock, and Douglas-fir trees of similar size growing on similar soils have roots that penetrate to similar depths and extend over similar areas *(10)*. Shallow root systems are most frequent where soil bulk density is high. Redcedar roots cannot grow in dense soils penetrated by the roots of Douglas-fir, red alder, lodgepole pine, and Pacific silver fir *(30)*. Redcedar root systems also tend to be shallower and less extensive on wet sites than they are on deep, moderately dry soils.

Where a thick duff layer is present, many redcedar roots lie in the duff rather than in the underlying soil. Root grafting is common *(9)*. Western redcedar mycorrhizae are of the vesicular-arbuscular type, and redcedar seedlings are more responsive to mycorrhizal inoculation than are the seedlings of redwood *(Sequoia sempervirens)*, incense-cedar *(Libocedrus decurrens)*, and giant sequoia *(Sequoiadendron giganteum) (27)*.

Reaction to Competition—Only Pacific silver fir, western hemlock, and Pacific yew are more tolerant of shade than western redcedar *(30)*. Its relative tolerance may be higher in warm than in cool areas, but redcedar is very tolerant wherever it grows, and it may be "the species of choice" for reforesting high, brush-risk areas near the coast *(6)*. Often present in all stages of forest succession, redcedar occupies pioneer, seral, and climax positions *(39)*. Multiple attributes seem to be responsible—redcedar invades disturbed areas as widely distributed seeds but regenerates vegetatively in undisturbed areas, tolerating competition in both *(26)*. Nevertheless, it is usually considered a climax or near climax species.

Western redcedar is best managed on moist sites characterized by the presence of ladyfern, queenscup, mountain woodfern, oakfern *(Gymnocarpium dryopteris)*, or thimbleberry. On poorly drained sites of lower quality, fertilizing with nitrogen appears to benefit growth *(37)*. Urea seems to be a better source of that nitrogen than ammonium nitrate *(54)*. Redcedar can be grown in stands of mixed species where uneven-aged management is practiced or when redcedar poles are to be produced under normal even-aged management regimes. But pure stands are more suitable for the long rotations needed to produce large sawtimber, shingles, and shakes.

Where western redcedar is managed in mixed-species or uneven-aged stands, its excellent shade tolerance and long life should be considered. Redcedar is usually overtopped by Douglas-fir, grand fir, western hemlock, and western white pine. It tolerates understory conditions in mixed-species stands but often grows slowly there. In uneven-aged stands, western redcedar can maintain acceptable growth rates over long periods, but it should not be given excessive crown space. Thinning from above may release the redcedars in mixed-species stands; thinning from below is preferable in uneven-aged stands of western redcedar. In the northern Rocky Mountains, growth response to release is best on large, young redcedars with green-yellow foliage growing on northerly aspects *(17)*. Redcedars probably should not be released when overtopped, however, because much of the increased growth after their release often occurs in large branches and a spreading crown rather than stem wood *(37)*.

Most western redcedars are harvested by clearcutting the mixed-species stands in which they grow. Because of steep terrain, decay, and breakage, redcedar harvesting costs are high and lumber recovery is low *(55)*. Redcedars should not be left as scattered seed trees, however; even those along clearcut margins may be lost to windthrow or exposure. Effects of slash-burning vary with site conditions, but low-impact spring burns tend to benefit the mycorrhizal colonization of seedlings *(6)*.

Damaging Agents—Western redcedar is less susceptible than its associates to most damaging agents, but, as it is longer lived, damaged trees are common. Although they are as windfirm as Douglas-fir on dry sites, redcedars are often windthrown in wet environments and are not resistant to windthrow on the moist sites where growth and yield are highest. Fire resistance also varies with environment. Redcedar is more severely damaged by fire than any of its associates along the coast but is less susceptible than Engelmann spruce, western hemlock, and subalpine fir in the interior *(30)*.

Western redcedar suffers little damage from insects, but it is a host for several economically important insect species *(13)*. One of the most important is the gall midge, *Mayetiola thujae*, which sometimes seriously damages redcedar seeds in Oregon, Washington, and British Columbia. Newly planted seedlings are occasionally damaged by a weevil *(Steremnius carinatus)* in British Columbia, and larger trees are killed by a bark beetle *(Phloeosinus sequoiae)* on poor sites in southeastern Alaska. The western cedar borer *(Trachykele blondeli)* causes degrade and cull in sawtimber.

More than 200 fungi are found on western redcedar, but it is less susceptible to pathological attacks than are most of its associates. Indeed, redcedar may be a suitable alternative species on coastal Douglas-fir and western hemlock sites where soils are infected with *Phellinus weiri*, *Fomes annosus*, or *Armillaria* spp. *(37)*. Nevertheless, many attacks occur during the long lives of some redcedar trees, and the heartwood extractives that provide decay resistance are eventually detoxified through biodegradation by a series of invading fungi *(25)*. As a result, the volume of accumulated decay in living trees is greater for western redcedar than for any other major conifer in British Columbia *(25)*, and hollow old trees are common in the interior *(7)*.

The major seedling disease, *Didymascella thujina*, is a leaf blight that infects 2nd- and 3rd-year nursery seedlings. As much as 97 percent of the natural redcedar reproduction may also be killed when this blight reaches epidemic proportions *(2)*. Epidemics are rare in North America, however, and *Didymascella* is not as damaging here as it is in Europe, where the disease seriously limited production of planting stock until cycloheximide fungicides were developed *(3,52)*.

In North America, the most important fungi attacking redcedar are root, butt, and trunk rots *(23)*. The root and butt rots include *Phellinus weiri*, *Armillaria mellea*, and *Poria subacida*. *Poria asiatica* and *P. albipellucida* are the most important trunk rots near the coast; *P. asiatica* and *Phellinus weiri* are most important in the interior range of western redcedar *(2)*. These rots are most evident in old stands, where much of the standing volume is often defective and unmerchantable.

Redcedar seedlings and saplings are often severely browsed by deer, elk, or rodents, and browse damage may be the most important stand-establishment problem *(6)*.

Western redcedar is damaged more than Sitka spruce by salt spray. Its foliage is more severely damaged by sulfur dioxide than is the foliage of Douglas-fir, western hemlock, and Sitka spruce and less damaged than the foliage of subalpine fir and grand fir. Redcedar is damaged less than Douglas-fir by airborne fluorides and ozone *(30)*.

Special Uses

Shingles and shakes constitute the most important special use of redcedar. Attractive appearance, durability, lightness, and superior insulation qualities probably are responsible for its popularity as a roofing material. Wood is also used in utility poles, fenceposts, piling, paper pulp, clothes closets and chests, caskets, crates, boxes, beehives, and fish-trap floats. Perfumes, insecticides, medicinal preparations, veterinary soaps, shoe polishes, and deodorants are made from cedar leaf oil. Redcedar extractives and residues are used in lead refining, boiler-water additives, and glue extenders *(31)*. When properly trimmed, redcedars make excellent hedges. Their drooping branches, thin fibrous bark, and flat sprays of scalelike leaves make redcedars attractive ornamental trees. The leaves are a major winter food for big game in the northern Rocky Mountains, and deer browse redcedar all year along the coast.

Genetics

Population Differences

Western redcedar seems to vary less than other northwestern conifer species. Lack of isoenzyme variation in newly germinated seedlings from western Oregon and eastern and western Washington indicates that redcedar populations contain little genetic polymorphism *(5)*. Isoenzyme variability is also low in British Columbia *(56)*. Leaf oil terpene composition is similar in populations at both low and high elevations in British Columbia, Washington, Oregon, Idaho, and Montana; but small differences between coastal and interior populations were recently detected by discriminant analysis of the chemical data *(53)*. Seedlings from different seed sources usually have remarkably similar forms and growth rates when grown in the same environment. Inland populations are more tolerant of frost than those from coastal populations, however *(46)*, and plantation trials indicate that provenances from Alaska are inferior to those from Oregon and Idaho when grown in Poland *(31)*. Seed orchards have been established in Denmark, where resistance to leaf blight and frost have been shown to be homozygously recessive *(52)*.

Races

Several horticultural varieties of western redcedar are grown in North America. They include *atrovirens*, *fastigiata*, and *pendula*. Haploid and triploid varieties have been studied in Germany *(31)*.

Hybrids

Thuja plicata × *Thuja standishii* hybrids are resistant to the leaf blight caused by *Didymascella thujina (52)*.

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Torreya taxifolia Arn. Florida Torreya

Taxaceae Yew family

Richard Stalter

Florida torreya *(Torreya taxifolia)* is an endangered species. This small rare tree is nearly extinct in the wild, threatened by a fungal disease of the stem. Known locally as stinking-cedar because of the pungent odor given off when the leaves are crushed, it was first discovered in 1833 by H. B. Croom near the Aspalaga Crossing on the Apalachicola River. Its rarity limited its use except locally for fenceposts and Christmas trees. The largest living specimen is in North Carolina and measures about 89 cm (35 in) in d.b.h., 14 m (45 ft) in height, with a crown spread of 12 m (40 ft).

Habitat

Native Range

Florida torreya (fig. 1) grows naturally in three counties in Florida, Gadsden, Liberty, and Jackson. It is also found in southern Decatur County, GA, just north of Chattahoochee, FL. The natural range of this species extends along the limestone bluffs for a 64-km (40-mi) stretch on the eastern bank of the Apalachicola River and its tributaries from Chattahoochee south to Torreya State Park in northern Liberty County, FL. One population exists approximately 11 km (7 mi) west of the Apalachicola River in the vicinity of Ocheessee Pond in Jackson County, FL.

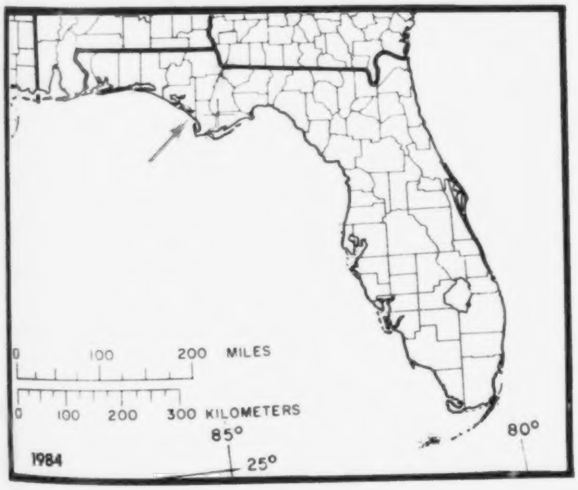

Figure 1—*The native range of Florida torreya.*

Climate

The climate of the region in the Florida Panhandle where *Torreya taxifolia* grows is warm and humid, with a wet summer and dry fall and winter. Average rainfall is 810 to 860 mm (32 to 34 in) during the growing season from April 1 to September 30, while the average yearly rainfall totals 1420 mm (56 in). The growing season averages 270 days. Killing frosts usually occur between November 25 and February 28. The average January temperature is 12° C (54° F), while the average July temperature is 27° C (81° F). Occasional cold waves in the winter bring a minimum temperature of -9° to -7° C (15° to 20° F). A low of -19° C (-2° F) has been recorded in Tallahassee, 64 km (40 mi) east of the Apalachicola River (10).

Soils and Topography

Florida torreya is restricted to steep, deeply shaded limestone slopes and wooded ravines. Soils in these areas most likely fall within the orders Alfisols and Mollisols.

Associated Forest Cover

Florida torreya (fig. 2) is not included among the forest cover types established by the Society of American Foresters but is commonly known to be among the oak-gum-cypress or oak-pine types. In 1919, it made up about 4 percent of the forest along the Apalachicola River. The most commonly associated species are beech *(Fagus grandifolia)*, yellow-poplar *(Liriodendron tulipifera)*, American holly *(Ilex opaca)*, Florida maple *(Acer barbatum)*, loblolly pine *(Pinus taeda)*, spruce pine *(P. glabra)*, white oak *(Quercus alba)*, eastern hophornbeam *(Ostrya virginiana)*, and sweetgum *(Liquidambar styraciflua)*. Shrubs and lianas associated with Florida torreya are poison-ivy *(Toxicodendron radicans)*, greenbriar *(Smilax* spp.), crossvine *(Bignonia capreolata)*, yaupon *(Ilex vomitoria)*, Florida yew *(Taxus floridana)*, blackberry and dewberry *(Rubus* spp.). Forbs, grasses, and sedges include sedges *(Carex*

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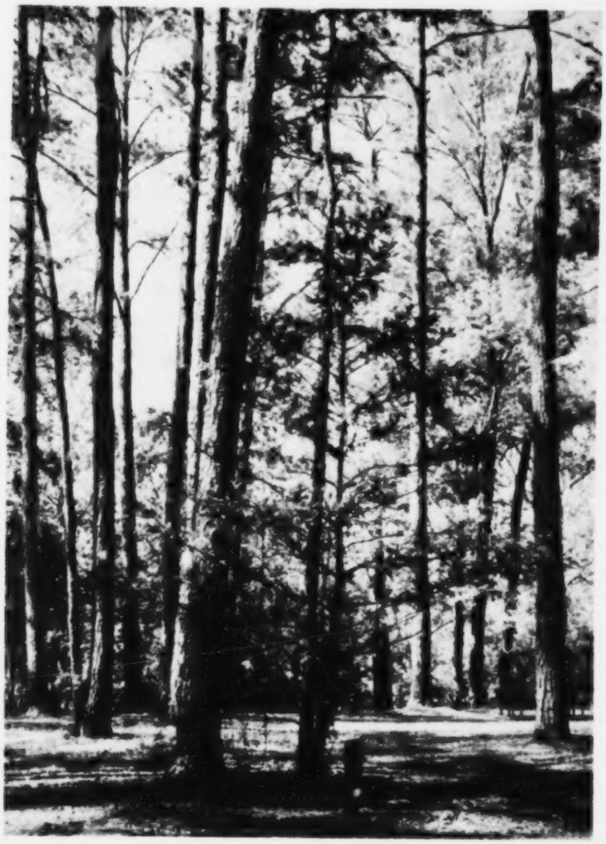

Figure 2—*Florida torreya about 6 m (20 ft) tall and 9 cm (3.5 in) in d.b.h.*

spp.), panic grass *(Panicum* spp.), partridgeberry *(Mitchella repens)*, little sweet Betsy *(Trillium cuneatum)*, giant cane *(Arundinaria gigantea)*, and American climbing fern *(Lygodium palmatum) (4,5,6)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Florida torreya is dioecious. Female flowers are produced in March and April and the ovule develops in a sessile, arillate structure. At the end of the second season, the fertilized ovule forms a single, nearly globose gray-blue fruit 2.5 to 4.1 cm (1.0 to 1.6 in) long, 1.9 to 3.6 cm (0.75 to 1.4 in) wide, which matures as early as August or as late as early November. Staminate cones are also initiated in March and April. These are small, globular-ovate, and bear four pollen sacs on each scale. *Torreya taxifolia* first produces male and female cones at age 20 *(2,8,9)*.

Seed Production and Dissemination—Little is known about germination of *Torreya taxifolia* seeds; they may germinate without stratification. According to R. Bowden at the Maclay State Gardens in Tallahassee, FL, some seeds germinated when placed in rich, damp topsoil. At Maclay, Bowden is currently investigating the physiological requirements for *Torreya taxifolia* germination. He has obtained 80 percent germination of 35 seeds by placing them in wet sphagnum moss *(2)*. Germination is hypogeal. *Torreya taxifolia* requires an after-ripening period before germination as does its closest American relative, *T. californica (8,9)*.

Seedling Development—Little is known about seedling development because few seedlings have been produced in the wild since the species was infected by a blight in the late 1950's. Perhaps mycorrhizae are beneficial to seedling establishment and growth. Seedlings in their natural habitat have developed in the deep shade of hardwoods and pines.

Vegetative Reproduction—Florida torreya can perpetuate itself vegetatively by producing sprouts at the base of the parent tree, although, in almost every instance, only one sprout survives after several years. Probably every existing Florida torreya in its present native habitat is a product of vegetative reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield—The bark on mature trees is about 1.3 cm (0.5 in) thick and irregularly divided by shallow fissures. The dark-brown outer bark often is tinged with orange while the inner bark is yellow. The twigs are green and stiff. The leaves are green, lustrous, stiff, and pungent. The common name, stinking-cedar, is derived from the disagreeable odor given off when any part of the tree is bruised.

Florida torreya is a small tree with whorled branches, reaching [illegible]2 m (40 ft) in height and 30 to 50 cm (12 to 20 in) in d.b.h. Its habitat on steep bluffs and its small stature and low population have made its exploitation impractical, and the species has never been commercially important *(3,8)*.

Rooting Habit—Florida torreya seedlings have a well-branched taproot. A 5-cm (2-in) seedling produces a taproot 5 cm (2 in) long. No information is available on root growth and the development of mature trees.

Reaction to Competition—Florida torreya appears to grow better in full sunlight at the Maclay State Gardens than in the dense shade of its natural habitat. It may most accurately be classed as tolerant of shade in its native habitat. No information on competition is available, however.

Damaging Agents—Godfrey and Kurz examined populations of *Torreya taxifolia* in 1962 and observed that many trees were infected by fungi that cause a stem and needle blight. They reported that many areas where the species previously thrived contained only a few skeletal trunks, some with abortive sprouts at their bases. The fungi responsible for the blight appear to be *Physalospora* spp. and *Macrophoma* spp., but investigators have not determined precisely how the fungal agents act to cause the blight. There is speculation that a sexual stage of the causal agent may be necessary to establish the infection and that the condition or age of the tree may be the important factor. Researchers found that the commercial fungicide Maneb at a concentration of 671 g per 378 liters (1.5 lb per 100 gal) applied at weekly intervals resulted in good control over 9 weeks of treatment, and that treated trees recovered markedly and produced new growth with little or no infection *(1,5)*.

Special Uses

Florida torreya has finely grained wood that is light, hard, strong, and durable. Its specific gravity is 0.5145. Because of its durability, it was formerly used for fence posts. Florida torreya have been cut for Christmas trees, but in 1980 and 1981 there were only a few Florida torreya tall enough to be used for this purpose *(7)*. Observation indicates that animals frequently eat torreya seeds *(8,9)*.

Genetics

No population differences have been observed in this species. No natural hybrids occur because this species is separated from its nearest North American relative, *T. californica*, by more than 2090 km (1,300 mi).

If Florida torreya is to be preserved, it will be necessary to isolate and propagate blight-resistant trees. Such genetic material may be propagated from *Torreya taxifolia* cuttings because they root readily. Once the seedlings are well established, they may be outplanted in suitable habitats along the Apalachicola River.

A number of diseased Florida torreya up to 9 m (30 ft) in height are growing in the Maclay State Gardens, FL. There are 14 disease-free specimens on the Biltmore Estate, Asheville, NC, that are more than 40 years old and up to 12 m (40 ft) tall but it is unlikely that they are blight resistant. Seeds and cuttings from the Biltmore Estate should be used to perpetuate disease-free trees inside and outside the species' natural range. All of the species at the Maclay Gardens as well as any accessible trees in their natural habitat should be treated for fungal infection if *Torreya taxifolia* is not to become extinct.

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Tsuga canadensis (L.) Carr. Eastern Hemlock

Pinaceae Pine family

R. M. Godman and Kenneth Lancaster

Eastern hemlock *(Tsuga canadensis)*, also called Canada hemlock or hemlock spruce, is a slow-growing long-lived tree which unlike many trees grows well in shade. It may take 250 to 300 years to reach maturity and may live for 800 years or more. A tree measuring 193 cm (76 in) in d.b.h. and 53.3 m (175 ft) tall is among the largest recorded. Hemlock bark was once the source of tannin for the leather industry; now the wood is important to the pulp and paper industry. Many species of wildlife benefit from the excellent habitat that a dense stand of hemlock provides. This tree also ranks high for ornamental planting.

Habitat

Native Range

The northern limit of eastern hemlock (fig. 1) extends from outliers in northeastern Minnesota and the western one-third of Wisconsin eastward through northern Michigan, south-central Ontario, extreme southern Quebec, through New Brunswick, and all of Nova Scotia. Within the United States the species is found throughout New England, New York, Pennsylvania, and the middle Atlantic States, extending westward from central New Jersey to the Appalachian Mountains, then southward into northern Georgia and Alabama. Outliers also appear in extreme southern Michigan and western Ohio, with scattered islands in southern Indiana and east of the Appalachians in the middle Atlantic States.

The range completely overlaps that of Carolina hemlock *(Tsuga caroliniana)*, a closely related species limited to the slopes of the Appalachians from Virginia and West Virginia into Georgia.

Commercial volumes of eastern hemlock have been greatly reduced by harvesting. In Michigan, for example, sawtimber volume decreased 69 percent and growing stock volume decreased 71 percent between 1935 and 1955 *(10)*. Both the type area and volume are continuing to decline because of harvesting and failure to regenerate, particularly in the western portion of the range. The remaining sawtimber is concentrated in the Northeast and the Lake States *(5)*.

Climate

Eastern hemlock is generally restricted to regions with cool humid climates. In the northern areas January temperatures average about -12° C (10° F) and July temperatures about 16° C (60° F). Precipitation ranges from less than 740 mm (29 in) in heavy snowfall areas of the north to more than 1270 mm (50 in) per year, about one-half occurring as summer precipitation. In the more productive areas near the Atlantic coast and southern Appalachians, January temperatures range as high as 6° C (42° F) and annual precipitation exceeds 1520 mm (60 in). The frost-free period is less than 80 days at the northern limits and nearly 200 days in the eastern and southern portions of the range.

Fully stocked stands of eastern hemlock tend to develop similar microclimates because of their dense canopy, dense shading, deep duff layer, and subsequent retention of moisture and uniformly low temperatures. In the few stands in which understories do develop, the type of vegetation tends to be similar to other forest types in the area although fewer species become established *(30)*.

Soils and Topography

The soil requirements for eastern hemlock are not exacting *(35)*. They are universally characterized as being moist to very moist but with good drainage. In the Lake States the species grows on upland sandy loams, loamy sands, and silt loams, often with an abundance of ground or coarse rocky material throughout the upper profile deposited from glacial or fluvial material. In Canada and the northeastern States the soils under eastern hemlock tend to be shallow loams and silt loams, often over granite, gneiss, and slate bedrock (Typic, Lithic, and Entic Haplorthods of the order Spodosols). Typically, most soils are highly acid, particularly in the upper horizons, but some are near neutral. The heavy, slowly decomposing litter fosters podzolization or leaching as the stand increases in age. On sites in which eastern white pine *(Pinus strobus)* is a major component, the soils tend to be of a sandy texture, well mixed with humus, moist, and well drained (Alfic Haplorthods). Scattered patches of hemlock also occur on the finer glacial tills as well (Alfic Fragiorthods), but in general these soils have less hemlock than the coarser soils.

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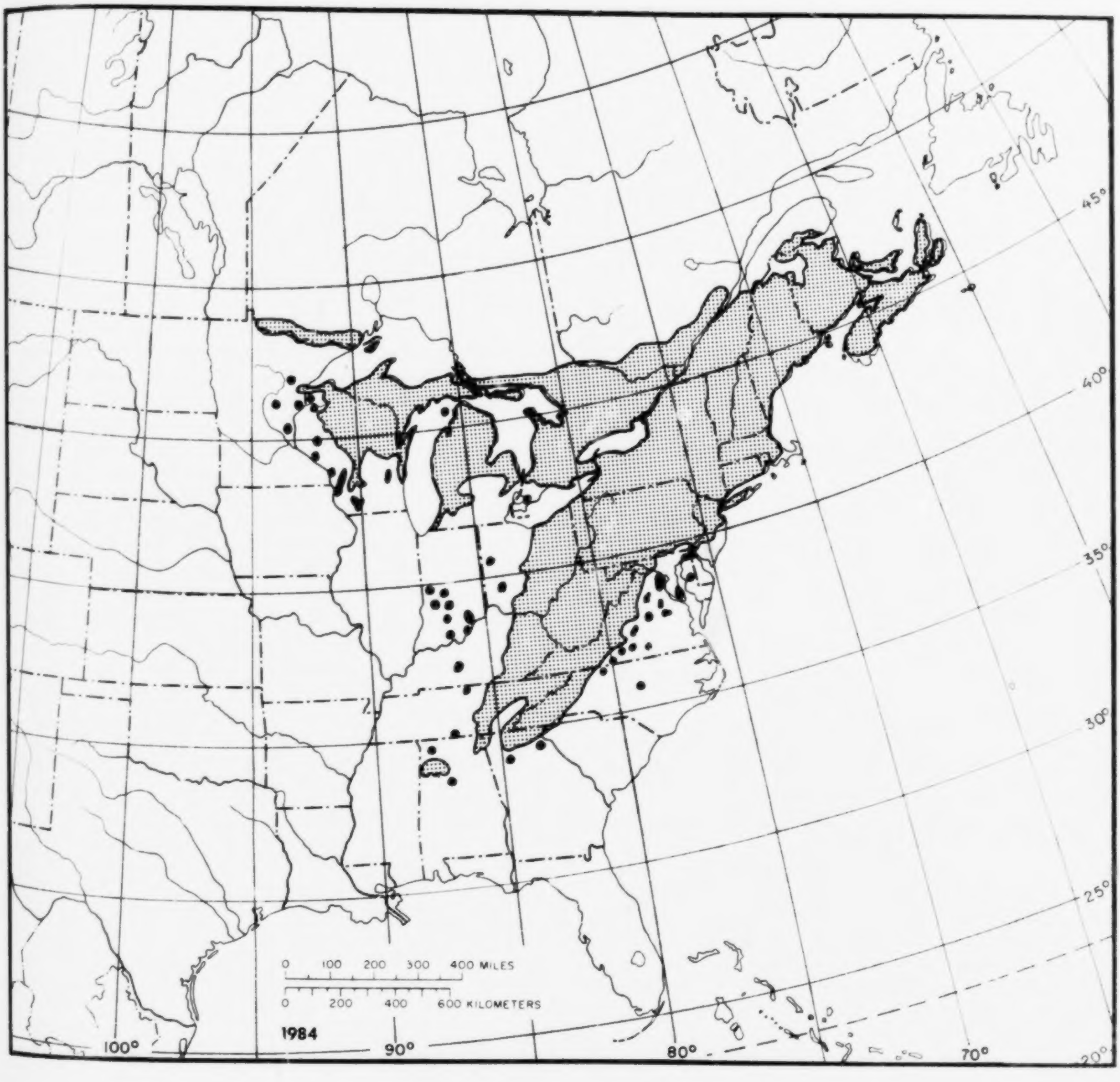

45°
40°
35°
30°
25°
20°
0 100 200 300 400 MILES
0 200 400 600 KILOMETERS
1984
100°
90°
80°
70°

Figure 1—*The native range of eastern hemlock.*

Eastern hemlock grows from sea level to about 730 m (2,400 ft) in elevation in the northeastern and northern portions of the range. Most commonly it is found on benches, flats, and swamp borders, provided the peat and muck soils are shallow (Aquic Haplorthods or Aeric Haplaquods). On the Allegheny Plateau, especially in New York and Pennsylvania, most of the hemlock grows between 300 and 910 m (1,000 and 3,000 ft) *(35)*. In the southern Appalachians the most frequent occurrences are at elevations of 610 to 1520 m (2,000 to 5,000 ft) and often are restricted to north and east slopes, coves,

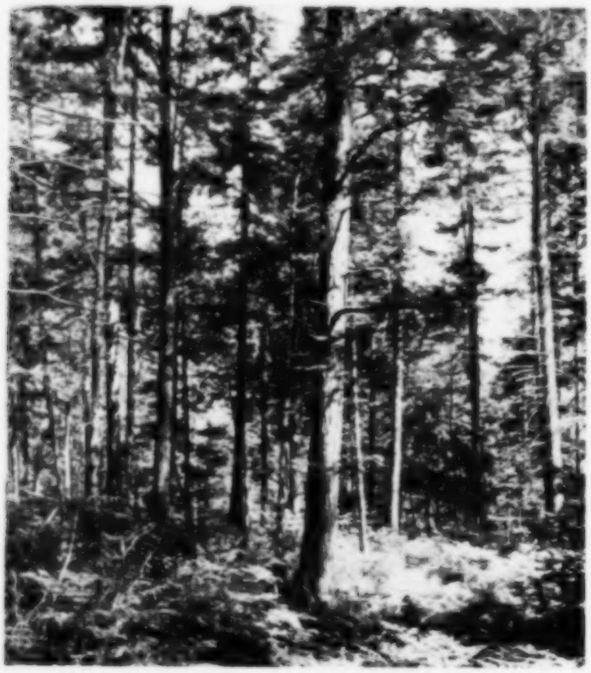

Figure 2—*Eastern hemlock in a red spruce–hemlock selection cut in Maine.*

or cool, moist valleys *(35)*. Outliers tend to be severely restricted by a combination of edaphic and climatic factors.

Associated Forest Cover

Eastern hemlock (fig. 2) is a major component of four forest cover types *(9)*: In the Northern Forest Region, White Pine–Hemlock (Society of American Foresters Type 22), Eastern Hemlock (Type 23), and Hemlock–Yellow Birch (Type 24); in the Central Forest Region, Yellow-Poplar–Eastern Hemlock (Type 58). It is also a common associate in seven types of the Northern Forest Region: White Pine–Northern Red Oak–Red Maple (Type 20), Eastern White Pine (Type 21), Red Spruce–Yellow Birch (Type 30), Red Spruce–Sugar Maple–Beech (Type 31), Red Spruce (Type 32), Red Spruce–Balsam Fir (Type 33), Red Spruce–Fraser Fir (Type 34). Eastern hemlock occurs in the following 18 types but only as a minor species:

5	Balsam Fir
17	Pin Cherry
18	Paper Birch
25	Sugar Maple–Beech–Yellow Birch
26	Sugar Maple–Basswood
27	Sugar Maple
28	Black Cherry–Maple
35	Paper Birch–Red Spruce–Balsam Fir
37	Northern White-Cedar
39	Black Ash–American Elm–Red Maple
44	Chestnut Oak
52	White Oak–Black Oak–Northern Red Oak
53	White Oak
57	Yellow-Poplar
59	Yellow-Poplar–White Oak–Northern Red Oak
60	Beech–Sugar Maple
97	Atlantic White-Cedar
108	Red Maple

Fully stocked stands of eastern hemlock form such a dense canopy that an understory seldom is able to develop. When an understory does exist, the most common herbs are false lily-of-the-valley *(Maianthemum canadense)*, starflower *(Trientalis borealis)*, woodfern *(Dryopteris* spp.), common woodsorrel *(Oxalis montana)*, goldthread *(Coptis groenlandica)*, clubmoss *(Lycopodium* spp.), and sedges *(Carex* spp.). Common mosses are *Dicranum* and *Polytrichum* *(30,39)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Flowering in eastern hemlock is monoecious with the flowers in separate clusters on the same branch. Beginning about age 15, male strobili arise from short-stalked light-yellow flower clusters in the axis of needles from the preceding year; they are then surrounded by bud scales to form the male conelet. The shorter ovulate flowers develop on the terminals of the previous year's branchlets and develop into erect conelets. Two ovules occur on each of the bracts. The time of flowering ranges from late April to early June, depending on the locality and season.

Pollen usually is dispersed by the wind beginning about 2 weeks after leaf buds burst, when the bracts on the female conelet are partially open *(28,29,35)*. At the close of pollination receptivity, the conelets are in a drooping position and the cone scales reclose. Fertilization is complete in about 6 weeks. During this period the pollen is extremely sensitive to drying, often the cause of seed failure *(28)*. Cones reach full size in late August to early September, about the same time as the winter buds begin to form. Cones open fully in mid-October, and seed dispersal extends into the winter. Opened cones may persist on the trees for slightly more than 1 year.

Seed Production and Dissemination—Cones of eastern hemlock are the smallest in the genus, from 13 to 19 mm (0.5 to 0.75 in) long; 35.2 liters (1 bushel) of cones weigh about 15.4 kg (34 lb), and yield from 0.64 to 0.68 kg (1.4 to 1.5 lb) of seed. The number of cleaned seeds ranges from 56,250 to 163,290/kg (25,500 to 74,070/lb). Seeds from eastern and southern areas are usually larger than those from northern and western regions. The seeds of eastern hemlock are slightly larger than those of western hemlock (*Tsuga heterophylla*) but are smaller than those of either Carolina or mountain hemlock (*T. mertensiana*) *(36)*. The single seeds are about 1.6 mm (0.06 in) long with a slightly longer terminal wing.

Seeds ripen about the time the cones change from yellowish green to purple brown. Dispersal of the seeds begins when the cones turn deeper brown indicating a reduction in moisture content. Most seeds fall within tree height because of the small wings. Additional distribution may occur from drifting on crusted snow. Some seeds may remain in the cones through the winter but usually they are sterile, having developed without an embryo *(35)*. In healthy, vigorous seeds, the embryo extends the full length of the seed.

Eastern hemlock is one of the most frequent cone producers among the eastern conifers. Good or better cone crops occur 61 percent of the years, based on 32 years of observation in Wisconsin *(13,29,37)*. Successive good or better cone crops did occur for one 5-year period and successive poor cone crops for a maximum of only 2 years. Excellent cone production has been reported for trees more than 450 years of age *(35)*.

Seedling Development—Despite the high frequency of cone crops and the long duration of cone production by individual trees, the viability of eastern hemlock seed is usually low. Germinative capacity commonly is less than 25 percent *(36)*. In one locality only 2.1 viable seeds were produced per cone, 2.2 were destroyed by insects, and the remaining 8.0 seeds were empty *(29)*.

Eastern hemlock seed is partially dormant at maturity and must be stratified about 10 weeks at or slightly above freezing temperatures for best germination. Unstratified seed must be exposed to light to break the partial dormancy. Under natural conditions the chilling requirements are met during the winter and the spring germination seldom is delayed because of seed dormancy *(35)*. Germination is epigeal.

The temperature requirements for germination of eastern hemlock are more exacting than for other species in the genus. A constant temperature of 15° C (59° F) is about optimum for germination. High germination percentages usually occur at temperatures ranging from 7° to 18° C (44° to 64° F), depending on the seed source *(29,35)*. These temperatures are nearly identical to those required for yellow birch (*Betula alleghaniensis*), the most common associated species in the northern region, and help to explain the association of two species differing so much in tolerance. Achieving desirable temperatures for germination under natural conditions is difficult because eastern hemlock seeds require from 45 to 60 days to reach their peak in germinative energy. Contrary to common belief, the species requires a warm, moist site for stand establishment rather than the cool, moist conditions that usually develop as stands mature.

Eastern hemlock seeds are easily damaged by drying. In one study 60 percent of the seeds were severely damaged after only 2 hours of drying, and 80 percent died or did not recover after 6 hours of drying *(35)*. Drying of the seedling after germination caused heavy root mortality that could not be overcome once moisture conditions improved.

Natural stands of eastern hemlock nearly always contain a large component of relatively even-aged trees but consistently have a stocking of older age classes and larger diameter trees that provided shelter during the regeneration period *(17,33,35,39)*. Consequently, new stands of eastern hemlock and yellow birch can be established under a high density overstory (from 70 to 80 percent crown cover) using the shelterwood regeneration system. The site must be prepared, however, by thorough mixing of organic and mineral soil or by prescribed fire to expose a partially decomposed layer *(6,12,14,18,26,32,34,35,38)*. Under this system, optimum conditions are created for germination and seedling establishment. Without these conditions most eastern hemlock regeneration is restricted to rotten logs, stumps, and mounds that normally have warmer surfaces and better moisture retention than the forest floor.

The rigid overstory and seedbed requirements for successful natural regeneration of eastern hemlock were evident in a direct seeding study in northwestern Pennsylvania. "No hemlock germinated on prepared spots in the open (hemlock rarely germinates and becomes established in open areas) and only a few germinated under a light overstory because of the moisture stress created under these conditions." Germination was good, however, on prepared sites under a pole-size stand, especially on north slopes *(20)*.

Under ideal growing conditions, seedlings of eastern hemlock develop slowly. First-year seedlings may grow only 25 to 38 mm (1 to 1.5 in) in height and the roots extend less than 13 mm (0.5 in) into the soil. These conditions provide moisture in the upper soil horizon throughout the growing season. "Because of their stable moisture requirements, seedlings are very sensitive to high temperatures and drying of the surface soil during the establishment period. Once the root system has reached a soil depth not radically affected by surface drying, usually after the second year, the seedlings grow more rapidly without interference of overhead shade. Seedlings are fully established when they are 0.9 to 1.5 m (3 to 5 ft) tall and at that time, can be released completely from overhead competition without fear of mortality."

Eastern hemlock seedlings are subject to damping-off as well as root rot fungi *(23,35)*. The fungi may be present in the soil or within the seed before it is dispersed. At least seven species of fungi are known to attack the seed, and several other species cause damping-off. Treatment of seeds with fungicides is frequently ineffective in controlling diseases and also delays or reduces germination. The high incidence of seedling disease combined with low seed viability suggest that supplemental seeding would enhance natural seeding under most conditions.

Vegetative Reproduction—None of the hemlocks sprout and only rarely layer. Vegetative propagation by cuttings and grafting are limited to ornamental production *(35)*. Stem cuttings are easily rooted but auxin treatments will enhance the response under greenhouse conditions. Natural root grafts have been reported in northern Wisconsin.

Most of the stock used in planting, both under forest conditions and as ornamentals, is grown from seed. Nursery grown seedlings grow slowly; 3-0 stock ranges from 13 to 23 cm (5 to 9 in) tall. Survival and height growth of planted hemlock, unlike natural regeneration, tend to be good both in the open and under partial overstories. Trees in a study in the Alleghenies grew significantly faster on north slopes under overstories of intermediate densities.

Sapling and Pole Stages to Maturity

Growth and Yield—Because early growth of eastern hemlock is so slow, trees less than 2.5 cm (1 in) in d.b.h. may be as old as 100 years and 5 to 8 cm (2 to 3 in) saplings may be 200 years old *(34)*. Growth during the pole stage also tends to be slow, mainly because of crowding and overstory suppression. One 26 cm (10.3 in) tree in a dense stand, for example, was 359 years old. Other trees of the same age in the dominant portion of the stand ranged from 61 to 91 cm (24 to 36 in) in d.b.h. Although many trees may be suppressed for as long as 200 years, they retain good stem form and live crown ratios.

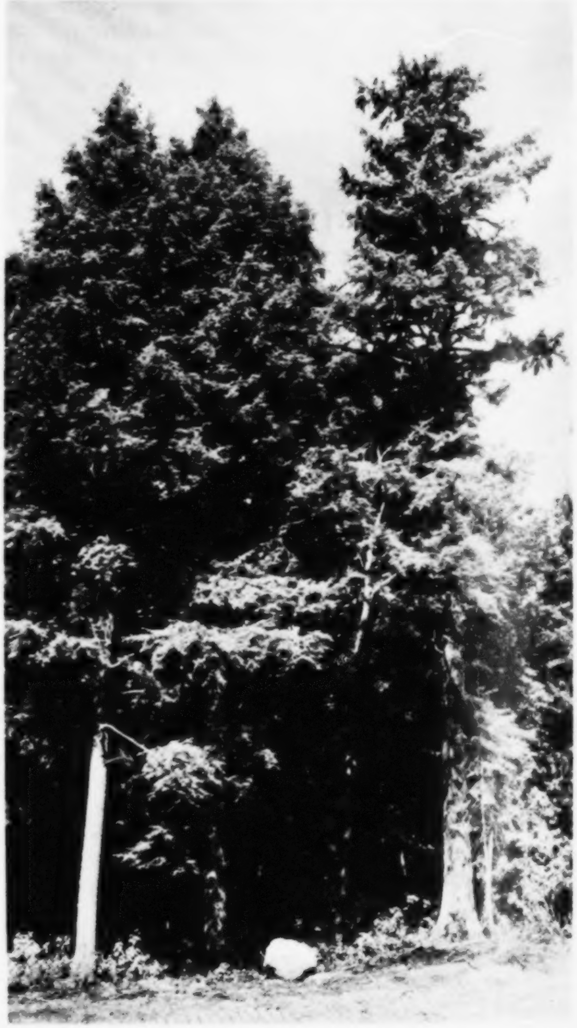

Figure 3—*A large forest-grown eastern hemlock.*

Mature eastern hemlock trees (fig. 3) attain relatively large diameters and height as well as retaining excellent stem form. The record age is reported to be 988 years, largest diameter 213 cm (84 in), and maximum height 49 m (160 ft) *(34)*. In typical stands, however, ages approaching 400 years, diameters of 89 to 102 cm (35 to 40 in), and heights in excess of 30 m (100 ft) are most common (table 1). "Accurate site index curves are not available for hemlock because most dominant trees have been suppressed during their early years, a result of the species' rigid

Table 1—Average dimensions of dominant eastern hemlock trees at selected locations

Age	Southern Applachians		Michigan		New York	
	D.b.h.	Height	D.b.h.	Height	D.b.h.	Height
yr	*cm*	*m*	*cm*	*m*	*cm*	*m*
40	23	16	14	13	11	12
60	33	22	24	19	19	18
80	43	26	33	23	27	22
100	52	30	41	26	35	26
120	62	33	49	28	43	28
140	71	35	57	29	52	30
160	81	37	65	30	61	31
180	91	38	—	—	70	—
200	100	39	—	—	78	—
yr	*in*	*ft*	*in*	*ft*	*in*	*ft*
40	9.0	53	5.7	42	4.4	39
60	13.1	71	9.4	62	7.4	58
80	16.3	86	12.8	76	10.5	73
100	20.6	98	16.1	85	13.8	84
120	24.3	107	19.4	91	17.1	91
140	28.0	114	22.6	96	20.4	97
160	31.9	120	25.7	100	23.9	102
180	35.7	125	—	—	27.4	—
200	39.5	129	—	—	30.9	—

overstory requirements for successful natural regeneration."

Yields of eastern hemlock tend to be higher than in most forest types except for white pine and red pine (*Pinus resinosa*). In New England, hemlock stands have about twice the volume of oak stands at 80 years of age but only from 50 to 60 percent of the volume of white pine stands at the same age (*35*). In northeastern Wisconsin on a typical loam podzol, well stocked hemlock and yellow birch stands attain volumes of 154 m³/ha (11,000 fbm) by age 110. On heavier soils, hemlock stands with a mixture of hardwoods reach volumes of 217 m³/ha (15,500 fbm) at 100 years. In pure, older stands gross volumes are reported in excess of 322 m³/ha (23,000 fbm) in Wisconsin and more than 560 m³/ha (40,000 fbm) in New England, but cull percent tends to increase rapidly in large diameter trees (*31,35*).

Rooting Habit—To a great extent, site conditions determine the rooting habits of eastern hemlock. When the watertable is near the surface, root systems are shallow. On better drained sites, deeper rooting patterns may be observed.

Reaction to Competition—Eastern hemlock is the most shade tolerant of all tree species (*3,15,35*). It can survive with as little as 5 percent of full sunlight, but under severe suppression only partial growth rings form and some may be missing entirely from the lower bole areas. In one study, from 10 to 40 rings were missing for a 120-year period of suppression. The tree is capable of withstanding suppression for as long as 400 years.

At all ages, however, eastern hemlock responds to release in both height and diameter growth. Growth rates in excess of 6.4 cm (2.5 in) per decade are possible following release either from side or overhead suppression. Excessive release often results in reduced growth and mortality and has been a contributing factor to partial uprooting or windthrow because of shallow rooting. Trees originating on logs or stumps often develop stilted root systems and also are susceptible to windthrow (*19*).

Even-aged or uneven-aged (selection) management systems can be successfully used to manage hemlock, but with certain limitations on the selection system. In the Lake States, the selection system has not always been successful and is not recommended for upland sites. In the East, the selection system has been used successfully on a limited basis, but the even-aged system is preferred and most frequently used.

A 2- or 3-cut shelterwood system is the best even-aged method for regenerating eastern hemlock. It is effective because it promotes seed germination and early seedling development by reducing moisture stress. However, the site must be properly scarified and all competing understory hardwoods removed to develop satisfactory seedbed conditions before or immediately after the first and sometimes the second cut.

In mixed stands of hardwoods and hemlock, where the proportion of hemlock is 15 percent or more, it is feasible to manage for hemlock, but at various residual stocking levels. Hemlock does not require as much growing space as hardwoods, so residual stocking is greater in stands where hemlock predominates. For example, a stand of trees averaging 25 cm (10 in) in diameter that contains 15 to 29 percent hemlock would be marked to favor hemlock at a residual stocking of about 22 m² (95 ft²) basal area of both hemlock and hardwoods. This same stand with 30 percent or more hemlock would be managed to 29 m² (125 ft²) of basal area. If less than 15 percent hemlock, the stand should be managed for the hardwood type represented.

Many fully stocked stands of eastern hemlock have basal areas in excess of 69 m²/ha (300 ft²/acre). When thinning heavily stocked stands—46 m²/ha (200 ft²/acre)—no more than one-third of the total basal area should be removed at one time. Excessive cutting results in reduced growth and increased mortality and contributes to windthrow. In addition, hardwood encroachment interferes with the successful establishment of hemlock. Fully stocked stands with densities less than 46 m²/ha (200 ft²/acre) can be thinned to a minimum of 27 m²/ha (120 m²/acre) without jeopardizing the residual stand *(22)*.

Acceptable standards for implementation of the uneven-aged system, based on field experience, include a residual stocking of 30 m²/ha (130 ft²/acre) in stands predominantly hemlock (50 percent or more); a stand structure (diameter distribution) of 35 percent poles 13 to 25 cm (5 to 10 in) d.b.h., and 65 percent sawtimber 30 cm (12 in) and larger. These guidelines will ensure a balanced growth between poletimber and sawtimber size classes. In addition, a continuous flow of ingrowth will occur and regeneration is assured if proper care is given to seedbed requirements.

Damaging Agents—Seeds of eastern hemlock are sensitive to damage from several molds, particularly *Botrytis* spp., that reduce or delay germination *(23)*. Some molds are borne internally while others colonize the seeds during germination. In one study, the fungus *Aureobasidum pullulans* was isolated from 73 percent of the seedcoats. In another test this mold was isolated twice from the embyronic tissue and 13 times from the seedcoat. Generally, molds are less injurious than desiccation during the germination and seedling stages.

The most damaging agents to young seedlings, other than desiccation, are damping-off fungi and root rots *(16)*. *Pythium* spp. and *Rhizoctonia* spp. flourish in wet, poorly drained soils and in well-drained soils, respectively, and are common on eastern hemlock. At least three root rots—*Cylindrocladium scoparium, Rhizina undulata* (common on burn areas), and *Fusarium moniliforme*—are common on eastern hemlock. *F. moniliforme* has been isolated from embryonic tissue and seedcoats as well as in the soil *(16,23)*.

Several diseases affect the needles and twigs of eastern hemlock. The rust caused by *Melampsora farlowii* is one of the most damaging. It causes shoot blight and curls and attacks the cone often resulting in cone abortion. Three rusts caused by *M. abietis-canadensis, Pucciniastrum hydrangeae,* and *P. vaccinii* spp. affect only the needles. Single needle browning throughout the crown is caused by *Fabrella tsugae*. Lower foliage in very wet and shady areas often has a grayish mat appearance on both the needles and twigs caused by *Rosellinia herpotrichioides*. *Dimerosporium tsugae* occasionally forms a black, sooty growth on the needles.

Living heartwood of eastern hemlock is attacked by *Tyromyces borealis*, particularly in the northeast, leaving white flecks in the wood. *Pholiota adiposa* is fairly common in the Lake States and causes a cavity along the pith axis. Other rots are the trunk rot caused by *Haematostereum sanguinolentum*; a brown, red ring rot caused by *Phellinus pini*; and a red heart rot caused by *P. robustus*. The red-varnish-topped fungus, *Ganoderma tsugae*, is the most common decayer of stumps and old logs.

Numerous fungi are associated with the root system but rarely develop conks or kill trees. The most common are the shoestring fungus, *Armillaria mellea*, and the velvet top fungi, *Phaeolus schweinitzii, Tyromyces balsameus*, and *Heterobasidion annosum*. At least two mycorrhiza are known to occur on the roots *(16)*.

Although at least 24 insects attack eastern hemlock, few are economically important. The most important is the hemlock borer, *Melanophila fulvoguttata*, which attacks weakened trees. Symptoms usually consist of woodpeckerlike holes in the bark, galleries filled with dark excrement, and yellowing shoot tips *(27)*. Spruce budworm, *Choristoneura fumiferana*, defoliates and kills hemlock after defoliating all the balsam fir in the stand.

The hemlock looper, *Lambdina fiscellaria fiscellaria*, devours part of the needle after which the remainder turns brown. In nurseries, white grubs of the strawberry root weevil, *Otiorhynchus ovatus*, consume the roots, and larvae of the black vine weevil, *O. sulcatus*, feed on the needles *(40)*. In the eastern States the hemlock scale, *Abgrallaspis ithacae*, damages young shade trees, and the gypsy moth, *Lymantria dispar*, kills understory trees.

Numerous animals feed on eastern hemlock and often cause serious damage, marked loss of vigor, or even death. White-tailed deer readily browse this species although it has been ranked seventh in winter food preference. In some regions, patches of regeneration have been eliminated following heavy browsing in years when deer populations are high. Although deer have been blamed for the absence of eastern hemlock in many localities, no regeneration occurred under similar conditions in fenced areas; thus, overstory–site–temperature requirements are presumably more critical *(2,6,8)*.

Snowshoe hares and New England cottontails frequently browse eastern hemlock. Mice, voles, squirrels, and other rodents also feed on seeds and small seedlings both under natural stands and in nurseries *(1)*. Porcupines occasionally gnaw the bark on larger trees causing serious wounds and top-kill *(4)*. Sapsuckers have been associated with ring shake in some areas *(19,21)*.

Small eastern hemlock trees are highly susceptible to wildfire but prescribed burns are beneficial for securing natural regeneration. The thick bark of older trees is resistant to light burns but saplings are usually destroyed. Root injury often occurs from high intensity fires because of heavy litter accumulation.

Drought is probably the most serious damaging agent to eastern hemlock, especially during the seedling stage. Winter drying caused by excessive transpiration on warm, windy days has caused severe needle injury.

In later stages of stand development, heavy cuttings predispose trees to windthrow because of their shallow rooting habit. Older trees are susceptible to radial stress cracks and ring shake, particularly in partially cut stands *(19)*. Eastern hemlock is sensitive to salt spray or drift and sulfur fumes and is one of the species most often struck by lightning *(16,25)*.

Special Uses

Lumber production from eastern hemlock reached its peak between 1890 and 1910. Primary uses were in light framing, sheathing, roofing, subflooring, boxes, crates, and general millwork. Much of the present production is used in pulping or newsprint and wrapping papers, but the demand for hemlock lumber appears to be increasing again.

Currently, eastern hemlock stands are considered essential for shelter and bedding of white-tailed deer during the winter. In regions of marked reductions in type area, many public agencies have restricted cutting until reliable methods of regenerating the stand become operational *(6)*. The type also is considered important as cover for ruffed grouse, turkeys, and many other animals.

Eastern hemlock often is planted as an ornamental because of its relative freedom from insects and disease, good foliage color, and adaptability to shearing. Some effort is being made to plant the species under forest conditions because it is so important to wildlife.

Tannin from the bark of eastern hemlock formerly was extracted for use in processing leather. Now synthetic and important products are used and a once prosperous industry has been eliminated *(19)*.

Genetics

Seedlings grown from 30 seed sources throughout the range showed a pattern of clinal variation in photoperiodic response. However, many species change abruptly when isolated on the basis of physiographic features *(35)*.

Comparison of an outlier source with one from Wisconsin indicated that races of eastern hemlock differ in physiological and morphological characteristics associated with locality *(7)*. No further studies have been reported on the genetics of eastern hemlock and no superior trees have been selected.

The primary effort in genetic research is propagation of variants for ornamental purposes. At least 280 clones are recorded as being variants, ranging from prostrate to weeping forms *(11)*.

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Tsuga heterophylla (Raf.) Sarg. Western Hemlock

Pinaceae Pine family

E. C. Packee

Western hemlock (*Tsuga heterophylla*), also called Pacific hemlock and west coast hemlock, thrives in humid areas of the Pacific coast and northern Rocky Mountains. Its potential for management as an efficient producer of fiber has long been recognized. It is an important browse species for deer and elk. Western hemlock provides an important part of the esthetic background for eight national parks—four each in the United States and Canada. It is a pioneer on many sites, yet it is commonly the climax dominant. Although western hemlock grows like a weed, its versatility and potential for management make it the "Cinderella of the Northwest."

Habitat

Native Range

Western hemlock (fig. 1) is an important commercial tree species of the Pacific coast and northern Rocky Mountains. Along the Pacific coast, its range extends north along the Coast Ranges from central California to the Kenai Peninsula in Alaska, a distance of 3200 km (2,000 mi) *(11,18,33)*. It is the dominant species in British Columbia and Alaska along the Coast Mountains and on the coastal islands.

Inland it grows along the western and upper eastern slopes of the Cascade Range in Oregon and Washington and the west side of the Continental Divide of the northern Rocky Mountains in Montana and Idaho north to Prince George, BC *(7,18,26)*.

Climate

Western hemlock thrives in a mild, humid climate where frequent fog and precipitation occur during the growing season. Best stands are in the humid and superhumid coastal regions. In subhumid regions with relatively dry growing seasons, western hemlock is confined primarily to northerly aspects, moist stream bottoms, or seepage sites.

Within the coastal range of western hemlock, mean annual total precipitation ranges from less than 380 mm (15 in) in Alaska to at least 6650 mm (262 in) in British Columbia. The range in the Rocky Mountains is 560 mm (22 in) to at least 1730 mm (68 in) *(25)*.

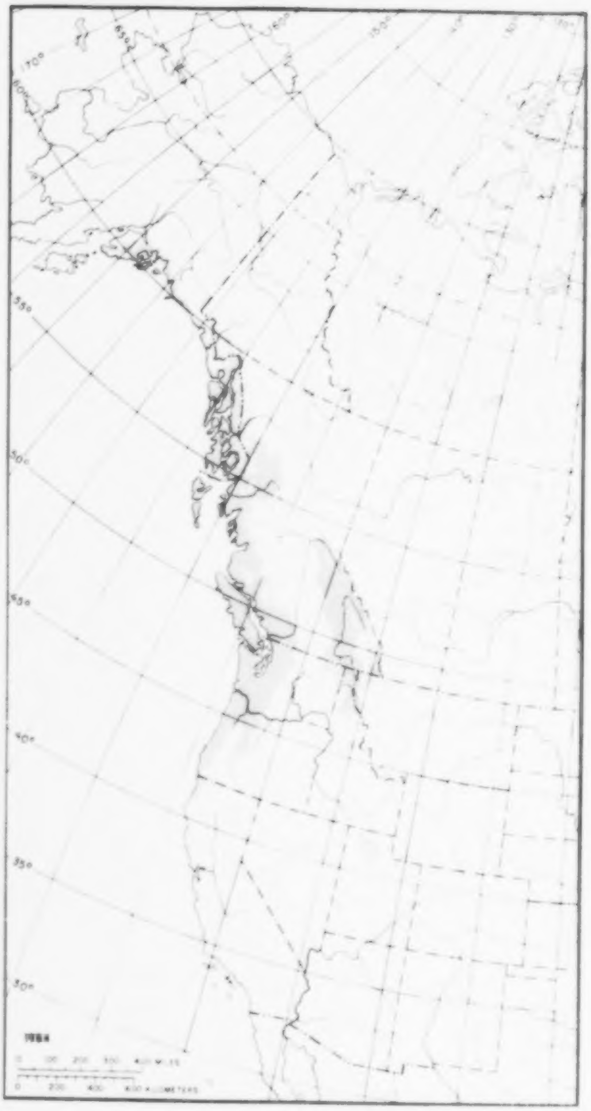

Figure 1—*The native range of western hemlock.*

Mean annual temperatures range from 0.3° to 11.3° C (32.5° to 52.3° F) on the coast and 2.2° to 8.2° C (36.0° to 46.8° F) in the Rocky Mountains. Observed mean July temperatures lie between 11.3°

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and 19.7° C (52.3° and 67.5° F) along the coast and 14.4° and 20.6° C (58.0° and 69.0° F) in the interior. Mean January temperatures reported for the two areas range from -10.9° to 8.5° C (12.4° to 47.3° F) and -11.1° to -2.4° C (12.0° to 27.6° F), respectively. Recorded absolute maximum temperature for the coast is 40.6° C (105.0° F) and for the Rocky Mountains, 42.2° C (108.0° F). Absolute minimum temperatures tolerated by western hemlock are -38.9° C (-38.0° F) for the coast and -47.8° C (-54.0° F) for the interior.

The frost-free period within the coastal range of western hemlock averages less than 100 to more than 280 days *(25)*. In the Rocky Mountains, the frost-free period is 100 to 150 days *(20)*.

Soils and Topography

Western hemlock grows on soils derived from all bedrock types (except possibly serpentines) within its range. It grows well on sedimentary (argillites, shales, sandstones, limestones), metamorphic (gneisses, marbles, quartzites, schists), and igneous (andesites, basalts, diorites, gabbros, granites) materials. Under appropriate climatic conditions, it thrives on all major landforms--colluvial, eolian, fluvial, lacustrine, marine, morainal, residual, rock, and organic.

Western hemlock grows on a variety of soils and is a characteristic species on soils of 6 of the 10 soil orders: Alfisols, Entisols, Histosols, Inceptisols, Spodosols, and Ultisols; and on many great groups, including: Fragiboralfs, Fragiudalfs, Hapludalfs; Fluvaquents, Udifluvents, Quartzipsamments; Borofolists, Cryolfolists; Cryandepts, Dystrandepts, Vitrandepts, Cryaquepts, Haplaquepts, Dystrochrepts, Cryumbrepts, Haplumbrepts; Fragiaquods, Placohumods, Cryorthods, Fragiorthods, Haplorthods; and Haplohumults. It is found on most soil textural classes. Height growth, however, decreases with increasing clay content or soil bulk density. This is attributed to inadequate soil aeration *(35)* or the inability of roots to penetrate compact soils.

Western hemlock thrives on soils with perudic and udic soil moisture regimes. If, however, internal soil drainage is restricted within 1 m (3.3 ft) of the soil surface, height growth decreases *(35)*. Western hemlock is poorly suited to sites where the water table is less than 15 cm (6 in) below the soil surface *(22)*. Although capable of existing on soils with moisture regimes tending toward ustic or xeric, it grows poorly; frequently, tops die back in years of drought.

The soil organic horizon under mature stands ranges from less than 7 to more than 57 cm (2.8 to 22.5 in); the average depth increases from 11.4 cm (4.5 in) on soils with good drainage to 43.2 cm (17.0 in) on poorly drained soils *(15)*. Commonly, the majority of roots, especially fine roots, are concentrated just below the organic horizon. The importance of the organic horizon as a continual supply of available nutrients for western hemlock cannot be overstated. In coastal British Columbia, earthworms are common in the organic horizons, even where the pH is less than 4; earthworms may play an important role in making nutrients available for root uptake. On many soils of Oregon and Washington, however, rooting depths exceed 1 m (3.3 ft).

Soil reaction (pH) under stands containing western hemlock ranges from less than 3.0 to nearly 6.0 in the organic horizons. The pH in the surface mineral horizons ranges from 4.0 to 6.3 and that of the C horizon from 4.8 to 6.2 *(21)*. Optimum range of pH for seedlings is 4.5 to 5.0.

Western hemlock is highly productive on soils with a broad range of available nutrients. Evidence from various locations on the Pacific coast suggests that the productivity of western hemlock increases as soil nitrogen increases *(15,21)*. There is no evidence that seedlings prefer ammonium over nitrate ions *(32)*. Phosphorus may be limiting on some sites as suggested by data from Oregon showing a strong relation between site index and soil phosphorus *(21)*. Although the requirement of western hemlock for cations is unclear, rooting habit and field data suggest that it requires or tolerates considerable amounts of calcium.

The range in elevation at which western hemlock grows is broad, from sea level to 2130 m (7,000 ft); its distribution varies by latitude and mountain range. On the coast, western hemlock develops best between sea level and 610 m (2,000 ft); in the Rocky Mountains, between 490 and 1280 m (1,600 and 4,200 ft) *(26)*.

Associated Forest Cover

Western hemlock (fig. 2) is either a major or a minor component in at least 20 forest cover types of the Society of American Foresters *(6)*.

		Pacific Coast	Rocky Mountains
202	White Spruce–Paper Birch	x	
205	Mountain Hemlock	x	x
206	Engelmann Spruce–Subalpine Fir		x
210	Interior Douglas-Fir		x
212	Western Larch		x
213	Grand Fir		x
215	Western White Pine		x
218	Lodgepole Pine	x	x
221	Red Alder	x	

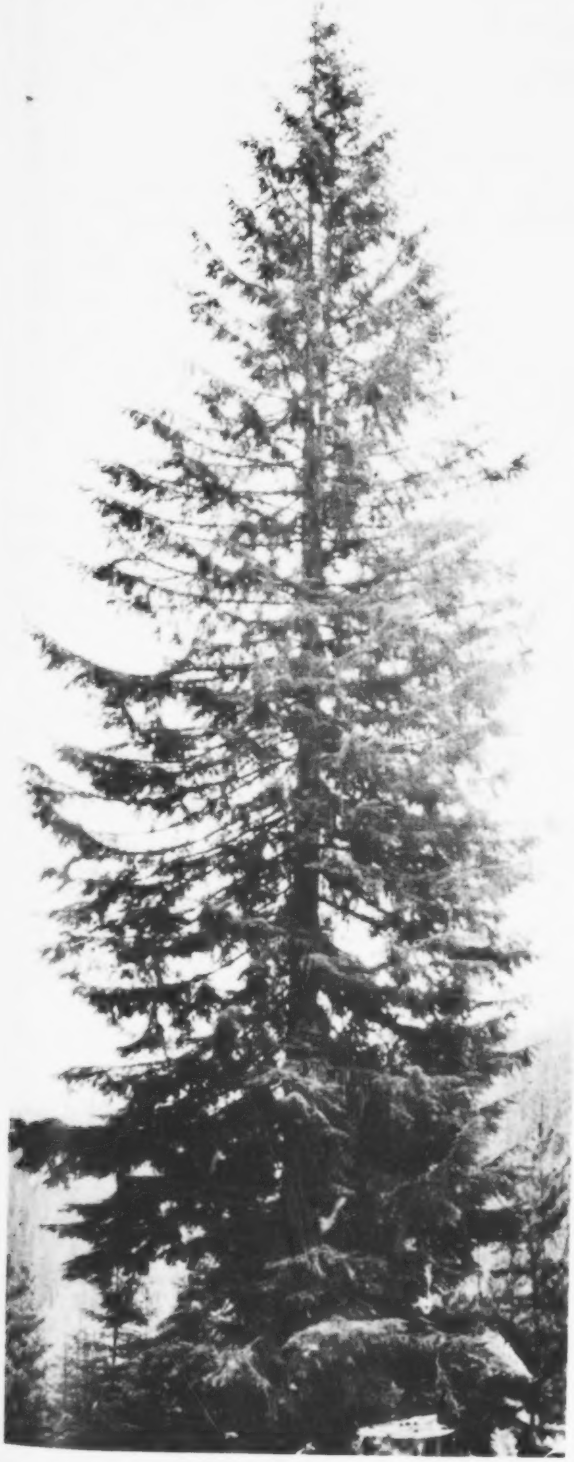

Figure 2—*Open-grown western hemlock, Coeur d'Alene National Forest, ID.*

	Pacific Coast	Rocky Mountains
222 Black Cottonwood–Willow	x	
223 Sitka Spruce	x	
224 Western Hemlock	x	x
225 Western Hemlock–Sitka Spruce	x	
226 Coastal True Fir–Hemlock	x	
227 Western Redcedar–Western Hemlock	x	x
228 Western Redcedar	x	
229 Pacific Douglas-Fir	x	
230 Douglas-Fir–Western Hemlock	x	x
231 Port Orford-Cedar	x	
232 Redwood	x	

The forest cover types may be either seral or climax.

Tree associates specific to the coast include Pacific silver fir (*Abies amabilis*), noble fir (*A. procera*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), giant chinkapin (*Castanopsis chrysophylla*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), Alaska-cedar (*C. nootkatensis*), incense-cedar (*Libocedrus decurrens*), tanoak (*Lithocarpus densiflorus*), Sitka spruce (*Picea sitchensis*), sugar pine (*Pinus lambertiana*), redwood (*Sequoia sempervirens*), and California laurel (*Umbellularia californica*). Associates occurring in both the Pacific coast and Rocky Mountain portions of its range include grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), paper birch (*Betula papyrifera*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), white spruce (*P. glauca*), lodgepole pine (*Pinus contorta*), western white pine (*P. monticola*), ponderosa pine (*P. ponderosa*), black cottonwood (*Populus trichocarpa*), Douglas-fir (*Pseudotsuga menziesii*), Pacific yew (*Taxus brevifolia*), western redcedar (*Thuja plicata*), and mountain hemlock (*Tsuga mertensiana*).

Western hemlock is a component of the redwood forests on the coasts of northern California and adjacent Oregon. In Oregon and western Washington, it is a major constituent of the *Picea sitchensis*, *Tsuga heterophylla*, and *Abies amabilis* Zones and is less important in the *Tsuga mertensiana* and Mixed-Conifer Zones (7). In British Columbia, it is a major element of the *Tsuga heterophylla–Picea sitchensis*, *Tsuga heterophylla–Abies amabilis*, *Tsuga heterophylla*, *Abies amabilis–Tsuga heterophylla*, and *Abies amabilis–Tsuga mertensiana* Vegetation Zones; it is confined to a distinct understory portion or to moist sites in the *Pseudotsuga menziesii–Tsuga heterophylla* and *Pseudotsuga menziesii* Zones (25). In the Rocky Mountains, it is present in the *Thuja plicata* and *Tsuga heterophylla* Vegetation Zones and the lower portion of the *Abies lasiocarpa* Zone (26).

Various persons have described the plant associations and biogeocoenoses in which western hemlock is found; more than 75 are listed for the west coast and more than 30 for the Rocky Mountains (25).

Little effort has been made to correlate the communities with one another.

Because of its broad range, western hemlock has a substantial number of understory associates. In its Pacific coast range, common shrub species include the following (starred species are also common associates in the Rocky Mountains): vine maple *(Acer circinatum)*, Sitka alder* *(Alnus sinuata)*, Oregongrape *(Berberis nervosa)*, snowbrush ceanothus* *(Ceanothus velutinus)*, salal *(Gaultheria shallon)*, oceanspray* *(Holodiscus discolor)*, rustyleaf menziesia* *(Menziesia ferruginea)*, devilsclub* *(Oplopanax horridus)*, Oregon boxwood* *(Pachistima myrsinites)*, Pacific ninebark* *(Physocarpus capitatus)*, Pacific rhododendron *(Rhododendron macrophyllum)*, stink currant *(Ribes bracteosum)*, prickly currant* *(R. lacustre)*, thimbleberry* *(Rubus parviflorus)*, salmonberry *(R. spectabilis)*, trailing blackberry *(R. ursinus)*, Pacific red elder *(Sambucus callicarpa)*, common snowberry* *(Symphoricarpos albus)*, Alaska blueberry *(Vaccinium alaskaense)*, big huckleberry *(V. membranaceum)*, ovalleaf huckleberry *(V. ovalifolium)*, evergreen huckleberry *(V. ovatum)*, and red huckleberry *(V. parvifolium)*. The following are other common associates in the Rocky Mountains: creeping western barberry *(Berberis repens)*, russet buffaloberry *(Shepherdia canadensis)*, birchleaf spirea *(Spiraea betulifolia)*, dwarf blueberry *(Vaccinium caespitosum)*, globe huckleberry *(V. globulare)*, and grouse whortleberry *(V. scoparium)*.

Common herbaceous species include the ferns: maidenhair fern *(Adiantum pedatum)*, ladyfern *(Athyrium filix-femina)*, deerfern *(Blechnum spicant)*, mountain woodfern *(Dryopteris austriaca)*, oakfern *(Gymnocarpium dryopteris)*, swordfern *(Polystichum munitum)*, and bracken *(Pteridium aquilinum)*. Herb associates include vanillaleaf *(Achlys triphylla)*, wild ginger *(Asarum caudatum)*, princes-pine *(Chimaphila umbellata)*, little princes-pine *(C. menziesii)*, queenscup *(Clintonia uniflora)*, cleavers bedstraw *(Galium aparine)*, sweetscented bedstraw *(G. triflorum)*, twinflower *(Linnaea borealis)*, Oregon oxalis *(Oxalis oregana)*, one-sided pyrola *(Pyrola secunda)*, feather solomonplume *(Smilacina racemosa)*, starry solomonplume *(S. stellata)*, trefoil foamflower *(Tiarella trifoliata)*, coolwort foamflower *(T. unifoliata)*, white trillium *(Trillium ovatum)*, roundleaf violet *(Viola orbiculata)*, evergreen violet *(V. sempervirens)*, and common beargrass *(Xerophyllum tenax)*.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Western hemlock is monoecious; male and female strobili develop from separate buds of the previous year. Female strobili occupy terminal positions on lateral shoots, whereas the male strobili cluster around the base of the needles *(4)*. Flowering and pollination begin from mid-April to late April in western Oregon and continue into late May and June in coastal Alaska. The solitary, long (19 to 32 mm; 0.75 to 1.25 in), pendent cones mature 120 to 160 days after pollination. Time of maturity of cones on the same branch is variable; ripe cones change from green to golden brown. The cone-scale opening mechanism does not appear to develop fully until late in the ripening period. Seeds are usually fully ripe by mid-September to late September, but cone scales do not open until late October. Empty cones often persist on the tree for 2 or more years.

Although flowering may begin on 10-year-old trees, regular cone production usually begins when trees reach 25 to 30 years of age. Mature trees are prolific producers of cones. Some cones are produced every year, and heavy crops occur at average intervals of 3 to 4 years; however, for a given location, the period between good crops may vary from 2 to 8 years or more. For example, in Alaska, good seed crops occur on an average of 5 to 8 years.

Seed Production and Dissemination—There are 56,760 to 83,715 cones per hectoliter (20,000 to 29,500/bu). Each cone contains 30 to 40 small seeds. Extraction and cleaning yields an average of 0.79 kg of seed per hectoliter (0.61 lb/bu) of cones. There are 417,000 to over 1,120,000 with an average 573,000 seeds per kilogram (189,000 to 508,000/lb; average 260,000). Slightly less than one-half of the seeds extracted from the cones are viable.

In coastal Oregon, more than 19.8 million seeds per hectare (8 million/acre) were released during each of two good seed years from 100-year-old stands, or about 30.3 kg/ha (27 lb/acre). In 1951, a hemlock–spruce stand in Alaska produced 96.4 kg/ha (86 lb/acre) of western hemlock seed. In the Rocky Mountains, western hemlock consistently produces more seed than its associates in the *Tsuga heterophylla Zone*.

Cone scales of western hemlock open and close in response to dry and wet atmospheric conditions. Under wet conditions, seed may be retained in the cones until spring. Western hemlock seed falls at a rate of 80 cm (31 in) per second *(27)*. Released in a strong wind, it can be blown more than 1.6 km (1 mi). In a wind of 20 km (12.5 mi) per hour, seed released at a height of 61 m (200 ft) traveled up to 1160 m (3,800 ft); most fell within 610 m (2,000 ft) of the point of release *(19)*. Seedfall under a dense canopy is 10 to 15 times greater than that within 122 m (400 ft) of the edge of timber in an adjacent clearcut.

Seedling Development—Western hemlock seeds are not deeply dormant; stratification for 3 to 4 weeks at 1° to 4° C (33° to 39° F) improves germination and germination rate. The germination rate is sensitive to temperature; optimum temperature appears to be 20° C (68° F). For each 5° C (9° F) drop below the optimum, the number of days required for germination is nearly doubled. Given sufficient time (6 to 9 months) and an absence of pathogens, western hemlock will germinate at temperatures just above freezing *(4)*. Germination is epigeal. Western hemlock seeds remain viable only into the first growing season after seedfall.

Provided adequate moisture is available, seed germination and germinant survival are excellent on a wide range of materials. Seeds even germinate within cones still attached to a tree. Western hemlock germinates on both organic and mineral seedbeds; in Alaska, establishment and initial growth are better on soils with a high amount of organic matter. Mineral soils stripped of surface organic material commonly are poor seedbeds because available nitrogen and mineral content is low.

In Oregon and Washington, exposed organic materials commonly dry out in the sun, resulting in the death of the seedling before its radicle can penetrate to mineral soil and available moisture. In addition, high temperatures, which may exceed 66° C (150° F) at the surface of exposed organic matter, are lethal. Under such moisture and temperature conditions, organic seedbeds are less hospitable for establishment of seedlings than mineral seedbeds *(27)*. Burning appears to encourage natural regeneration on Vancouver Island; after the third growing season, burned seedbeds had 58 percent more seedlings with better distribution than unburned seedbeds *(17)*.

Decaying logs and rotten wood are often favorable seedbeds for western hemlock. Decayed wood provides adequate nutrition for survival and growth of seedlings *(23)*. In brushy areas, seedlings commonly grow on rotten wood where there is minimum competition for moisture and nutrients. Seedlings established on such materials frequently survive in sufficient numbers to form a fully stocked stand by sending roots into the soil around or through a stump or log.

Because western hemlock can thrive and regenerate on a diversity of seedbeds, natural regeneration can be obtained through various reproduction methods, ranging from single-tree selection to clearcutting. Through careful harvesting of old-growth stands, advance regeneration often results in adequately stocked to overstocked stands.

Western hemlock is difficult to grow in outdoor nurseries. Container-grown stock appears to result in higher quality seedlings, less damage to roots, and better survival than does bare root stock.

Initial growth is slow; 2-year-old seedlings are commonly less than 20 cm (8 in) tall. Once established, seedlings in full light may have an average growth rate of 60 cm (24 in) or more annually.

Vegetative Reproduction—Western hemlock can be propagated by layering and from cuttings. Seedlings that die back to the soil surface commonly sprout from buds near the root collar. Sprouting does not occur from the roots or the base of larger saplings.

Western hemlock grafts readily. Incompatibility between the scion and rootstock does not appear to be a problem. Growth of grafted material is better than that of rooted material.

Sapling and Pole Stages to Maturity

Growth and Yield—Western hemlock (fig. 3) may form pure stands or be a component of mixed stands. Young stands vary in stocking, but understocking is infrequent. Natural 20-year-old stands can have 14,800 to 24,700 or more stems per hectare (6,000 to 10,000/acre). Stocking levels of 1,480 to 1,790 stems per hectare (600 to 725/acre) at crown closure are believed to provide the best yields if commercial thinnings are part of the management regime *(12)*. If thinnings are not planned, stocking levels as low as 740 well-distributed trees per hectare (300/acre) can provide maximum yields at rotation age *(27)*.

The response of western hemlock to nitrogen fertilizer is extremely variable. It appears to vary by geographic location and stocking level. For overstocked stands, a combination of precommercial thinning and fertilizer often gives the best response.

Comparative yield data from paired British plantations strongly suggest that western hemlock commonly outproduces two of its most important associates, Douglas-fir and Sitka spruce *(1)*. Natural stands of western hemlock along the Pacific coast attain appreciably higher yields than Douglas-fir stands having the same site index *(34)*; the weighted mean annual increment of western hemlock for some common forest soils in Washington is 33 to 101 percent more than the mean annual increment for Douglas-fir *(30)*. On the Olympic Peninsula, western hemlock out-produces Douglas-fir by 25 to 40 percent. Similar relationships occur in south coastal British Columbia *(12)*. The higher mean annual in-

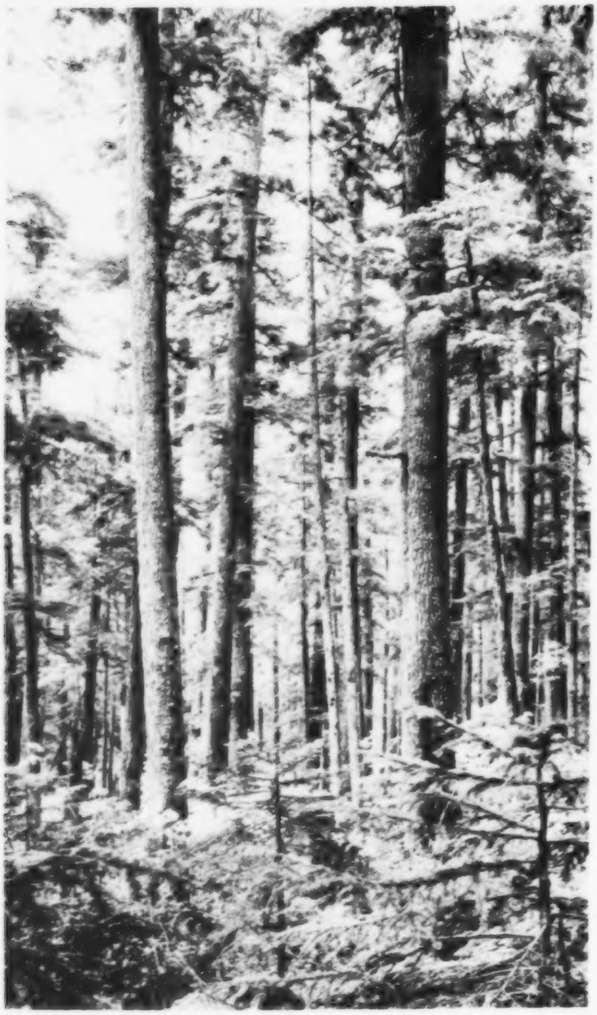

Figure 3—*A mature stand of western hemlock in Washington. Trees average about 76 cm (30 in) in d.b.h.*

crement of western hemlock apparently is due to the ability of western hemlock stands to support more trees per hectare; individual trees also have better form than other species and hence better volume (at least 4 to 14 percent) *(34)*.

Mixed stands of western hemlock and Sitka spruce are especially productive. In the *Picea sitchensis* Zone of Oregon and Washington, the mean annual increment of such stands frequently exceeds 42 m^3/ha (600 ft^3/acre). At higher elevations and farther north mixed stands of western hemlock and Pacific silver fir are also highly productive.

Yield data for natural stands are given in table 1. Volumes predicted for normally stocked stands may actually underestimate potential yields by 20 to 50 percent. Data from British Columbia suggest greater yields can be had if a high number of stems per hectare are maintained *(12)*. Yields of western hemlock on the best sites can exceed 1848 m^3/ha (26,400 ft^3/acre) at 100 years of age.

Western hemlock forests are among the most productive forests in the world. The biomass production of several western hemlock stands with a site index (base 100 years) of 43 m (140 ft) was investigated at the Cascade Head Experimental Forest near Lincoln City, OR. The biomass of standing trees of a 26-year-old, nearly pure western hemlock stand was 229 331 kg/ha (204,614 lb/acre) and that of a 121-year-old stand with a spruce component of 14 percent was 1 093 863 kg/ha (975,966 lb/acre). Net primary productivity per year for these two stands was estimated to be 37 460 and 22 437 kg/ha (33,423 and 20,019 lb/acre). Net primary productivity appears to peak at about 30 years, then declines rapidly for about 50 years. Foliar biomass in the stands at Cascade Head averages 22 724 kg/ha (20,275 lb/acre) with a leaf area of 46.5 m^2/m^2 (46.5 ft^2/ft^2) *(8, 10)*. By comparison, available data indicate much lower values for highly productive Douglas-fir stands—12 107 kg/ha and 21.4 m^2/m^2 (10,802 lb/acre and 21.4 ft^2/ft^2), respectively.

On the best sites, old-growth trees commonly reach diameters greater than 100 cm (39.6 in); maximum diameter is about 275 cm (108 in). Heights of 50 to 61 m (165 to 200 ft) are not uncommon; maximum height is reported as 79 m (259 ft). Trees over 300 years old virtually cease height growth *(27)*. Maximum ages are typically over 400 but less than 500 years. The maximum age recorded, in excess of 700 years, is from the Queen Charlotte Islands *(16)*. Several major associates (Douglas-fir, western redcedar, Alaska-cedar) typically reach much greater ages.

Rooting Habit—Western hemlock is a shallow-rooted species; it does not develop a taproot. The roots, especially the fine roots, are commonly most abundant near the surface and are easily damaged by harvesting equipment and fire.

Reaction to Competition—Western hemlock is rated to be very tolerant of shade. Only Pacific yew and Pacific silver fir are considered to have equal or greater tolerance of shade than western hemlock.

Western hemlock responds well to release after a long period of suppression. Advance regeneration 50 to 60 years old commonly develops into a vigorous, physiologically young-growth stand after complete removal of the overstory; however, poor response to release has been noted for suppressed trees over 100 years old. Advance regeneration up to 1.4 m (4.5 ft) tall appears to respond better to release than taller individuals. Because of its shade tolerance, it is an ideal species for management that includes partial cutting; however, if it is present and the management goal is for a less tolerant species, normal partial cutting practices are not recommended.

Under conditions of dense, even-aged stocking, early natural pruning occurs, tree crowns are usually narrow, and stem development is good. Given unrestricted growing space, the quality of western hemlock logs is reduced because of poorly formed stems and persistent branches. Trees that develop in an understory vary greatly in form and quality.

The successional role of western hemlock is clear; it is a climax species either alone or in combination with its shade-tolerant associates. Climax or near-climax forest communities along the Pacific coast include western hemlock, western hemlock–Pacific silver fir, western hemlock–western redcedar, Pacific silver fir–western hemlock–Alaska-cedar, and western hemlock–mountain hemlock. The longevity of some associates of western hemlock makes it difficult to determine if some of these near-climax communities will develop into pure western hemlock stands or if western hemlock will ultimately be excluded.

Climax or near-climax communities in the Rocky Mountains include western hemlock, western hemlock–western redcedar, and occasionally subalpine fir–western hemlock. In the last community, western hemlock plays a distinctly minor role *(26)*.

Damaging Agents—Many agents adversely affect the growth, health, and quality of western hemlock trees and stands.

Because of its thin bark and shallow roots, western hemlock is highly susceptible to fire. Even light ground fires are damaging. Prescribed burning is an effective means of eliminating western hemlock advance regeneration from a site.

Because of its shallow roots, pole-size and larger stands of western hemlock are subject to severe windthrow. Thousands of hectares of young stands dominated by coastal western hemlock have originated after such blowdown.

Western hemlock suffers frost damage in the Rocky Mountains, especially along the eastern edge of its range where frost-killed tops are reported *(20,26)*. Snowbreak occurs locally; it appears to be most common east of the Cascade and Coast Mountains, and especially in the Rocky Mountains. On droughty sites, top dieback is common; in some exceptionally dry years, entire stands of hemlock saplings die. Suddenly exposed saplings may suffer sunscald. Excessive amounts of soil moisture drastically reduce growth.

Table 1—Characteristics of fully stocked, 100-year-old western hemlock stands in Oregon (OR), Washington (WA), British Columbia (BC), and Alaska (AK) (adapted from *2*)

	Average site index at base age 100 years[1]				
Item	**61 m or 200 ft**	**52 m or 170 ft**	**43 m or 140 ft**	**34 m or 110 ft**	**26 m or 85 ft**
Avg. height, m					
OR/WA	58.8	49.7	40.8	31.7	—
BC	—	50.0	40.8	31.7	22.3
AK	—	—	38.4	29.3	20.7
Avg. d.b.h., cm					
OR/WA	58	54	49	42	—
BC/AK	—	44	40	31	22
Stocking[2], trees/ha					
OR/WA	299	339	400	526	—
BC/AK	—	482	573	865	1,384
Basal area[2], m^2/ha					
OR/WA	83.3	81.7	79.0	75.3	—
BC/AK	—	75.5	73.0	67.5	59.9
Whole tree volume[2], m^3/ha					
OR/WA	1771	1498	1218	938	—
BC	—	1449	1228	938	612
AK	—	—	1158	868	560
Avg. height, ft					
OR/WA	192.9	163.1	133.9	104.0	—
BC	—	164.0	133.9	104.0	73.2
AK	—	—	126.0	96.1	67.9
Avg. d.b.h., in					
OR/WA	23.0	21.4	19.2	16.5	—
BC/AK	—	17.5	15.6	12.4	8.8
Stocking[2], trees/acre					
OR/WA	121	137	162	213	—
BC/AK	—	195	232	350	560
Basal area[2], ft^2/acre					
OR/WA	362.9	355.9	344.1	328.0	—
BC/AK	—	328.9	318.0	294.0	261.0
Whole tree volume[2], ft^3/acre					
OR/WA	25,295	21,394	17,406	13,405	—
BC	—	20,693	17,549	13,405	8,746
AK	—	—	16,549	12,405	8,003

[1] Site indexes range within 4.6 m (15 ft) of the averages.

[2] Trees larger than 3.8 cm (1.5 in) in d.b.h.

Western hemlock is one of the species most sensitive to damage by sulfur dioxide *(16)*. Spring applications of the iso-octyl esters of 2,4-D and 2,4,5-T in diesel oil can kill leader growth of the last 3 years.

Severe fluting of western hemlock boles is common in southeast Alaska, much less common on Vancouver Island, and relatively uncommon in Washington and Oregon. There appears to be a clinal gradient from north to south; the causal factor is not known.

No foliage diseases are known to cause serious problems for western hemlock.

Dwarf mistletoe *(Arceuthobium tsugense)* is a serious parasite along the Pacific coast from California nearly to Glacier Bay, AK; its presence on western hemlock in the Rocky Mountain States is unconfirmed. It increases mortality, reduces growth, lowers fiber quality, and provides an entryway for decay fungi. Uninfected to lightly infected trees may have a greater growth in volume (40 percent) and height (84 percent) than severely infected trees; in mature stands, volume losses as high as 4.2 m^3/ha (60 ft^3/acre) per year have been reported *(29)*. Dwarf mistletoe in western hemlock is easy to control; success is nearly 100 percent if methods of sanitation are good.

Armillaria mellea, Heterobasidion annosum, Phaeolus schweinitzii, Laetiporus sulphureus, Inonotus tomentosus, Poria subacida, and *Phellinus weiri* are the major root and butt pathogens of western hemlock. *Armillaria mellea* occurs widely, seldom kills trees directly, and is not a major source of cull.

Heterobasidion annosum, the most serious root pathogen of western hemlock, can limit the alternatives available for intensive management *(3)*. The incidence of infected trees in unthinned western hemlock stands ranges from 0 to more than 50 percent. In some thinned stands, every tree is infected. *Heterobasidion annosum* spores colonize freshly cut stumps and wounds; the spreading mycelium infects roots and spreads to adjacent trees through root grafts. Treating stumps and wounds with chemicals can reduce the rate of infection.

Phellinus weiri is a common root pathogen where Douglas-fir is or was a major component of the stand. In the Rocky Mountains, a similar relationship may exist with western redcedar. *Phellinus weiri* rapidly extends up into the bole of western hemlock. The first log is frequently hollow; only the sapwood remains. The only practical controls for *P. weiri* are pulling out the stumps and roots or growing resistant species.

High risk bole pathogens include *Echinodontium tinctorium, Heterobasidion annosum,* and *Phellinus weiri*. *Echinodontium tinctorium* causes extensive decay in overmature stands in the Rocky Mountains. It is less destructive in immature stands, although it is found in trees 41 to 80 years old; 46 percent of the trees in this age group in stands studied were infected. *Echinodontium tinctorium* is of little consequence on the coast. *Heterobasidion annosum* spreads from the roots into the bole of otherwise vigorous trees. On Vancouver Island, an average of 24 percent (range 0.1 to 70 percent) of the volume of the first 5-m (16-ft) log can be lost to *H. annosum (24)*.

Rhizina undulata, a root rot, is a serious pathogen on both natural and planted seedlings on sites that have been burned. It can kill mature trees that are within 8 m (25 ft) of the perimeter of a slash burn *(3)*.

Sirococcus strobilinus, the sirococcus shoot blight, causes dieback of the tip and lateral branches and kills some trees in Alaska; the potential for damage is not known *(27)*.

Of the important insects attacking western hemlock, only three do not attack the foliage. A seed chalcid *(Megastigmus tsugae)* attacks cones and seeds; the larva feeds inside the seed. This insect normally is not plentiful and is of little consequence to seed production *(14)*. A weevil *(Steremnius carinatus)* causes severe damage in coastal British Columbia by girdling seedlings at the ground line. In the Rocky Mountains, the western larch borer *(Tetropium velutinum)* attacks trees that are weakened by drought, defoliated by insects, or scorched by fire; occasionally it kills trees *(9)*.

Since 1917, there have been only 10 years in which an outbreak of the western blackheaded budworm *(Acleris gloverana)* did not cause visible defoliation somewhere in western hemlock forests *(28)*. Extensive outbreaks occur regularly in southeast Alaska, on the coast of British Columbia, in Washington on the south coast of the Olympic Peninsula and in the Cascade Range, and in the Rocky Mountains. In 1972, nearly 166 000 ha (410,000 acres) were defoliated on Vancouver Island alone. Damage by the larvae is usually limited to loss of foliage and related growth reduction and top kill. Mortality is normally restricted to small stands with extremely high populations of budworms.

The western hemlock looper *(Lambdina fiscellaria lugubrosa)* has caused more mortality of western hemlock than have other insect pests. Outbreaks last 2 to 3 years on any one site and are less frequent than those of the budworm. The greatest number of outbreaks occurs on the south coast of British Columbia; the western hemlock looper is less prevalent farther north. Heavy attacks have been recorded for Washington and Oregon since 1889. The insect is less destructive in the interior forests. Although mortality is greatest in old growth, vigorous 80- to 100-year-old stands are severely damaged.

Two other loopers, the greenstriped forest looper (*Melanolophia imitata*) and the saddleback looper (*Ectropis crepuscularia*), cause top kill and some mortality. The phantom hemlock looper (*Nepytia phantasmaria*) in the coastal forest and the filament bearer (*Nematocampa filamentaria*) play minor roles, usually in association with the western hemlock looper *(28)*.

The hemlock sawfly (*Neodiprion tsugae*) occurs over most of the range of western hemlock. Its outbreaks often occur in conjunction with outbreaks of the western blackheaded budworm. The larvae primarily feed on old needles; hence, they tend to reduce growth rather than cause mortality *(9)*. The hemlock sawfly is considered the second most destructive insect in Alaska *(13)*.

Black bear girdle pole-size trees and larger saplings or damage the bark at the base of the trees, especially on the Olympic Peninsula of Washington. Roosevelt elk and black-tailed deer browse western hemlock in coastal Oregon, Washington, and British Columbia. The snowshoe hare and the brush rabbit damage hemlock seedlings, principally by clipping off the main stem; clipping of laterals rarely affects survival of seedlings *(5)*. Mountain beaver clip the stems and lateral branches of seedlings and girdle the base of saplings along the coast south of the Fraser River in British Columbia to northern California. Four years after thinning, evidence of girdling and removal of bark was present on 40 percent of the trees *(5)*. Mortality results from both kinds of damage.

Special Uses

The forest industry recognizes western hemlock as an all-purpose raw material. It treats well and is used for pilings, poles, and railway ties. Strength and nailing characteristics make it a preferred species for construction lumber in North America and overseas. Better lumber grades are used for appearance and remanufacture products. Western hemlock has good-to-excellent pulping characteristics and is an important fiber source for groundwood, thermomechanical, kraft, and sulfite pulps.

Genetics

A natural cross between western hemlock and mountain hemlock, *Tsuga* × *jeffreyi* (Henry) Henry, has been reported from the Mount Baker area in Washington. Analysis of polyphenolic pigment suggests that chemical hybrids between western hemlock and mountain hemlock occur but are rare. Intergeneric hybridization between western hemlock and spruce has been discussed in the literature; although similarities exist between the two genera, they do not suggest hybridization *(31)*.

Albino individuals or those similarly deficient in chlorophyll have been observed in the wild.

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Tsuga mertensiana (Bong.) Carr.   Mountain Hemlock

Pinaceae   Pine family

Joseph E. Means

Mountain hemlock *(Tsuga mertensiana)* is usually found on cold, snowy subalpine sites where it grows slowly, sometimes attaining more than 800 years in age. Arborescent individuals that have narrowly conical crowns until old age (300 to 400 years) and shrubby krummholz on cold, windy sites near timberline add beauty to mountain landscapes. Taylor and Taylor *(76)* thoroughly describe its form. Uses of its moderately strong, light-colored wood include small-dimension lumber and pulp.

Habitat

Native Range

Mountain hemlock (fig. 1) grows from Sequoia National Park in California (lat. 36° 38′ N.) *(62)* to Cook Inlet in Alaska (lat. 61° 25′ N.) *(83)*. It grows along the crest of the Sierra Nevada in California *(31)*; the Cascade Range in Oregon; the Cascade Range and Olympic Mountains in Washington; the northern Rocky Mountains in Idaho and western Montana; the Insular, Coast, and Columbia Mountains in British Columbia; and in southeast and south-central Alaska.

Climate

Areas occupied by mountain hemlock (fig. 2) generally have a cool to cold maritime climate that includes mild to cold winters, a short, warm to cool growing season and moderate to high precipitation (table 1). Annual and summer precipitation and the proportion of precipitation as snow show notable latitudinal climatic trends in the range of mountain hemlock (table 1). Latitudinal trends in mean temperatures are not evident.

The high snowfall results in snowpacks with maximum depths that range from 245 cm (96 in) in Idaho to 380 cm (150 in) in British Columbia *(9)*. A snowpack may cover the ground for long periods (7 to 10 months in southwestern British Columbia) *(9)*. The relatively short growing season (frost-free period) ranges from 95 to 148 days in southwestern British Columbia *(9,45)* and from 49 to 63 days in the central Sierra Nevada *(64)*.

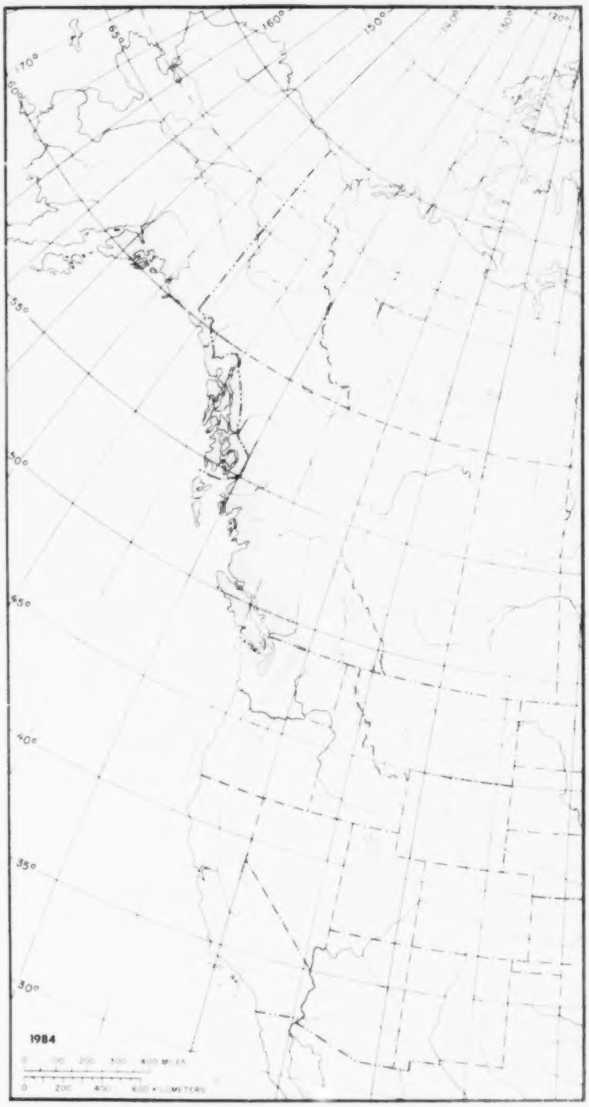

Figure 1—*The native range of mountain hemlock.*

Climatic extremes include a temperature range of -29° to 38° C (-20° to 100° F) *(11)*, annual snowfall in excess of 2200 cm (866 in) *(66)*, snowpack up to 750 cm (295 in) *(20)*, and persistence of the snowpack

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until August or September *(9,66)*. Because there are few weather stations in the range of mountain hemlock, reported extremes are probably often exceeded.

Mountain hemlock grows in an altitudinal band 300 to 1000 m (1,000 to 3,300 ft) wide that increases in altitude from north to south:

	Altitude	
	m	*ft*
Alaska *(83)*	0 to 1067	0 to 3,500
Northern British Columbia *(46)*	300 to 900	1,000 to 3,000
Southern British Columbia *(46)*	900 to 1800	3,000 to 5,900
Northern Washington *(20)*	1300 to 1700	4,200 to 5,600
Rocky Mountains *(12,33,63)*	1550 to 2100	5,100 to 6,900
Southern Oregon *(42)*	1600 to 2300	5,200 to 7,500
Northern Sierra Nevada *(64)*	2400 to 3050	7,900 to 10,000
Southern Sierra Nevada *(62)*	2750 to 3050	9,050 to 10,000

The presence of mountain hemlock in the Rocky Mountains is closely correlated with the eastward penetration of moist maritime air masses *(33)*. On the east side of the Coast Mountains in British Columbia, mountain hemlock is limited to relatively moist sites where snow accumulates early in the fall *(46)*. Krajina *(46)* proposes that mountain hemlock does not grow on sites with later, thinner snowpacks because it cannot tolerate the frozen soils there.

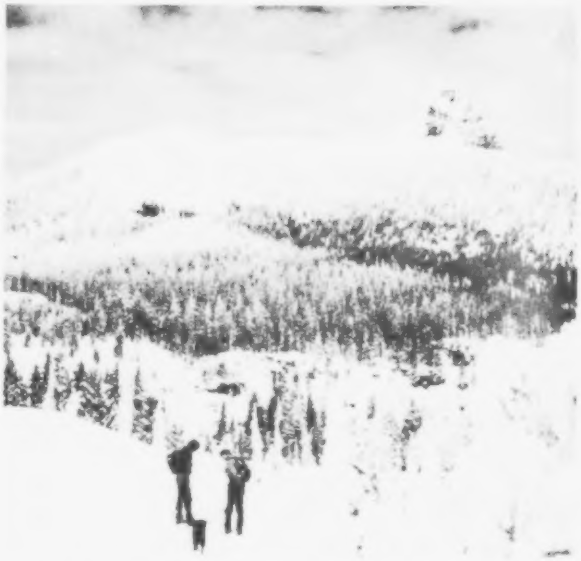

Figure 2—*Winter landscape in the subalpine mountain hemlock zone, high Cascades of Oregon. In the middle distance is a stand representative of the continuous forest subzone; above this and to the right is an example of the parkland subzone.*

Table 1—Climatological data from 14 weather stations within the range of mountain hemlock

Location and number of stations	Temperature			Precipitation		
	Annual	January	July	Annual	June to August	Portion[1] as snowfall
		°C		*mm*	*mm*	*pct*
Alaska,[2] 3	4	–7	13	1681	346	14
British Columbia, 4	3	–3	11	3021	361	29
Washington, 2	4	–3	12	2728	270	51
Northern Idaho, 1	3	–7	15	971	124	65
Oregon, 1	4	–4	13	1643	99	81
California, 3	3	–4	13	1048	51	88
		°F		*in*	*in*	*pct*
Alaska[2] *(80)*	39	20	56	62	13	14
British Columbia *(9,45)*	38	26	52	104	14	29
Washington *(20)*	39	27	53	107	11	51
Northern Idaho *(79)*	37	19	59	38	5	65
Oregon *(20)*	39	25	56	65	4	81
California *(64,77)*	38	24	56	39	2	88

[1] Estimated from snowfall by assuming 10 cm (4 in) of snow is equivalent to 1 cm (0.4 in) of rain, for all locations but those in British Columbia.

[2] Stations in Alaska are near sea level. Mountain hemlock grows at higher elevations where

Throughout most of the range of mountain hemlock local climate differentiates two types of subalpine mountain hemlock forest. A **parkland subzone** of single trees and small tree clumps (average canopy cover less than 25 percent) extends from treeline or near treeline to the lower **forest subzone** of relatively continuous forest cover (canopy cover more than 25 percent) *(2,9,21,82)*. Most climatic data (table 1) are from the forest subzone. Detailed microclimatic data *(9)* and data extrapolated upslope from the weather stations *(45)* in southwestern British Columbia indicate that the parkland subzone has shorter frost-free and snow-free periods and that maximum snowpack, range of summer temperatures, and actual evapotranspiration are greater than in the forest subzone. Mountain hemlock also grows above treeline in the alpine environment as prostrate krummholz (elfinwood) throughout most of its range *(10,20,35)*.

If climate warms as hypothesized for western North America *(24)*, existing mountain hemlock forests will probably increase in productivity; upper and lower boundaries of the mountain hemlock zone, within which new mountain hemlock forests become established after disturbance, will increase in elevation; and the zone will decrease in area. Near Mount Baker, Washington, ring width of mountain hemlock increases with increasing monthly temperatures in the preceding 12 months, decreasing winter precipitation *(37)*, and decreasing spring snow depth, down to about 1 m (3.3 ft) *(27)*. This implies productivity should increase with predicted temperature increases. Graumlich and others *(28)* estimated that productivity increased 60 percent in the last century in four high-elevation stands in Washington, three of which contained 48 to 96 percent mountain hemlock. They related this increase most strongly to the increase in growing-season temperature during this period (about 1.5° C or 2.7° F). Thus, further increases in temperature may cause further increases in productivity.

Based on the current elevational distribution of major forest zones in the Oregon Cascades and a mean temperature lapse rate of 4.4° C/100 m (2.4° F/1,000 ft), Franklin and others *(24)* have hypothesized the effects of two warmer climates. If mean annual temperature increases 2.5° C (4.5° F), the mountain hemlock zone in Oregon may be shifted upwards 570 m (1,900 ft) and decrease in area from 9 to 2 percent; an increase of 5.0° C (9° F) may move it upwards 1140 m (3,700 ft)—above all but the tallest peaks—so it is effectively eliminated.

Soils and Topography

Over its range, mountain hemlock grows on soils derived from a wide variety of parent materials, including those of volcanic, sedimentary, metamorphic, and glacial origin. It is, however, relatively rare and stunted on soils derived from calcareous parent materials in the Selkirk Mountains of British Columbia *(11)*. Mountain hemlock was not found on calcareous parent materials in the Rocky Mountains of the United States, but edaphic factors influencing its distribution in that area are not clear *(12,63)*.

Mountain hemlock is reported on organic soils (Histosols) in the northern portion of its range *(9,82)* more often than in the southern portion *(62,64)*. In Alaska it is found down to sea level on noncommercial forest land on organic soils bordering muskegs where it may be a major stand component *(35)*. A stunted or prostrate form is often found on these muskegs. It also grows below its usual altitudinal range in British Columbia on poorly drained sites where other species offer little competition *(11)*.

Best development of mountain hemlock is on loose, coarse-textured, well-drained soils with adequate moisture *(9,11,62)*, and in British Columbia *(9)*, on thick and very acidic organic matter and decayed wood. Adequate soil moisture appears to be especially important in California *(11,62)* and Montana *(33)*—portions of its range where summer drought is most pronounced. Mature soils typically found under mountain hemlock stands in Alaska, British Columbia, and Washington are Cryaquods and Cryorthods of the order Spodosols. These soils typically have a 13- to 28-cm (5- to 11-in) forest floor with a root mor or mycelial root mor humus layer in British Columbia *(9)*, and a 5- to 10-cm (2- to 4-in) forest floor with a mor or duff mull humus layer in the Washington Cascades *(20)*. In the central and southern Oregon Cascades and in northeastern Washington and northern Idaho, mature soils are generally weakly developed Haplorthods with densely matted felty mor humus layers 2 to 5 cm (1 to 2 in) thick *(12,20,90)*. Mountain hemlock also commonly grows on immature soils (Entisols and Inceptisols). For example, it grows on Andepts (soils derived from volcanic ash) in the Cascade Range in Oregon *(38,42)*. Forest floors and mineral soil surfaces of pumice and ash soils supporting mountain hemlock in Oregon show moderate resistance to wetting when dry *(42)*.

Stands dominated by mountain hemlock typically have very acidic forest floors (pH 3.4 to 5.0, rarely 6.0) and mineral soils (pH 4.2 to 6.2) with low base saturation (9 to 18, rarely 37 percent) in British Columbia *(9)*, Washington, Oregon *(77,90)*, and northern Idaho *(12)*. Mountain hemlock accumulates aluminum in its foliage and fine roots, so it may increase the acidity and speed up podzolization of these soils *(85)*. Total nitrogen in the forest floor (0.4 to 1.13 percent) and mineral soil (0.05 to 0.4 percent) in British Columbia *(9)*, Washington, and Oregon *(51,77,90)* are comparable to those of other coniferous forests in the region. Levels of available nitrogen in an old-growth stand in Oregon, as indexed by 7-day anaerobic 40° C (104° F) incubations, are extremely low in the mineral soil (1.7 to -2.3 µg N/g) and 100 times higher but still low in the forest floor (45 to 225 µg N/g) relative to levels for lower elevation stands in Oregon and Washington *(51)*. A study of forests on an altitudinal gradient in western Oregon indicates that, as for available nitrogen, a high proportion of soil calcium (98 percent), organic matter (50 percent), and total nitrogen (34 percent) is in the forest floor relative to most lower elevation forest types *(77)*. Because of this, nutrients in the forest floor are very important to the productivity of these forests. These edaphic differences are caused by slower (measured) decomposition rates caused in large part by lower temperatures and, on some sites, by the youth and infertility of the volcanic ash parent material.

Mountain hemlock will grow on most landforms, but individuals typically develop best in mixed stands of the forest subzone on sheltered slopes or in draws. From southern British Columbia south, the tree grows better on northerly exposures (*11*). The preference for relatively moist, cool sites evidently becomes a necessity as the climate becomes more continental in western Montana (*33*) and more mediterranean in the central Sierra Nevada (*62*) at these extremes of its range. In these locations, mountain hemlock typically grows in isolated populations in north-facing glens and cirque basins where snow collects and may remain well into summer.

Limited data on stomatal behavior from Carson Pass, CA, indicate that mountain hemlock is adapted to sites with long-lasting snowpacks. In the spring, mountain hemlocks emerging through 2 to 4 m (7 to 13 ft) of snow were transpiring and, presumably, photosynthesizing (*73*), whereas nearby whitebark pines (*Pinus albicaulis*) did not transpire until the soil beneath them was free of snow. Water uptake by seedlings in a greenhouse decreases to near zero at soil water potential of about -2 MPa (versus about -3 MPa for Douglas-fir) because of greater uptake resistance (*5*). Such decreases suggest that mountain hemlock is less well adapted to droughty sites or sites with high evaporative demand.

Associated Forest Cover

The mountain hemlock zone includes the upper Canadian and most of the Hudsonian Life Zones (*11*) and includes all of the forest cover type Mountain Hemlock (Society of American Foresters, Type 205) (*16*). Mountain hemlock is a major component of Coastal True Fir–Hemlock (Type 226), California Mixed Subalpine (Type 256) and (in the Cascade Range) Whitebark Pine (Type 208). Mountain hemlock is a minor associate in 12 other coniferous types: Engelmann Spruce–Subalpine Fir (Type 206), Red Fir (Type 207), Interior Douglas-Fir (Type 210), Western Larch (Type 212), Western White Pine (Type 215), Lodgepole Pine (Type 218), Sitka Spruce (Type 223), Western Hemlock (Type 224), Western Hemlock–Sitka Spruce (Type 225), Western Redcedar–Western Hemlock (Type 227), Western Redcedar (Type 228), and Port-Orford-Cedar (Type 231).

Mountain hemlock usually grows in mixture with other trees, and it has many associates, as is evident from the large number of forest types in which it is found. Though pure stands are less common than mixed stands, there are extensive pure stands of mountain hemlock in Alaska (*11*) and in the central high Cascades of Oregon (*20*).

One of the most widespread mountain hemlock communities is the mountain hemlock–Pacific silver fir/big huckleberry (*Tsuga mertensiana–Abies amabilis/Vaccinium membranaceum*) type found in British Columbia (*9*) and the Oregon and Washington Cascades (*1,20*). In British Columbia, the understory is dominated by deciduous ericaceous shrubs: Cascades azalea (*Rhododendron albiflorum*), Alaska huckleberry (*Vaccinium alaskaense*), rustyleaf menziesia (*Menziesia ferruginea*), ovalleaf huckleberry (*Vaccinium ovalifolium*), and big huckleberry. Also included are strawberryleaf blackberry (*Rubus pedatus*) and several mosses. Silver fir and Alaska-cedar (*Chamaecyparis nootkatensis*) are common tree associates in this community in coastal areas, and subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are common associates in inland areas (*9*).

In the Rocky Mountains, the mountain hemlock/beargrass (*Xerophyllum tenax*) habitat type is generally found on south slopes and is characterized by a high cover of beargrass with big huckleberry and grouse whortleberry (*Vaccinium scoparium*) as common associates (*12,63*). Subalpine fir and lodgepole pine (*Pinus contorta*) are common arborescent associates. A similar Pacific silver fir–mountain hemlock/beargrass association is found in Oregon (*20*).

The extensive pure or nearly pure mountain hemlock forests in the high Cascades of Oregon are primarily in the mountain hemlock/grouse whortleberry community (*38,42,48,72*). Except for grouse whortleberry, understory plant cover is generally low, long-stoloned sedge (*Carex pensylvanica*) being the most commonly mentioned associate.

Mountain hemlock forests in Crater Lake National Park were classified with 89 percent accuracy using Landsat imagery (*86*), which offers hope for broad-scale mapping of this forest type.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Mountain hemlock is monoecious. Pollen release occurs in June in the Cascade Range in Oregon (*11*), from mid-June to mid-July in British Columbia (*14,61*), and from mid-May to late June in Alaska. In a British Columbia study, mountain hemlock and subalpine fir were the last of 10 species to release pollen (*14*). Daytime temperature appeared to be the most important variable regulating release of pollen, with more release (and by inference more pollination) on warm, dry days. Both protogyny (*53*) and synchrony between pollen release and female cone receptivity on individual trees have been observed in British Columbia. Fertilization occurs from about late July to early August in British Columbia (*61*). Reproductive buds can easily be identified in the late summer and fall (*15*).

Many female strobili indicate the potential for a large cone crop next year. Mature cones are oblong, purple or brownish purple, and are generally longer than the other species of *Tsuga* (2 to 9 cm or 0.75 to 3.5 in) *(53)*. Owens and Molder *(60)* have thoroughly described the reproductive cycle of mountain hemlock.

Seed Production and Dissemination—Three years of data from British Columbia indicate that high temperatures in July the year before cone production favor cone-bud initiation *(14)*. Cones ripen and open from late September to November *(11,61)*. Wild mountain hemlock as young as 20 years may bear cones *(11,65)*. A study of cone-bud initiation indicates it may be possible to induce cone production at younger ages *(58)*. Mature trees 175 to 250 years old produce medium to very heavy cone crops at about 3-year intervals in Oregon and Washington but crops may be complete failures in other years *(22)*. Mountain hemlock seeds are dispersed primarily by wind. During a bumper mountain hemlock seed year in Oregon, seedfall at the clearcut-forest boundary was very high (215,000 to 4,144,000/ha or 87,000 to 1,677,000/acre) and was greatest at the south edge and least at the north edge of a gently sloping 12.5-ha (31-acre) clearcut *(21)*. Seedfall was correlated with stand basal area in this study, as basal areas at the north and south edges were 34 and 94 m^2/ha (149 and 410 ft^2/acre), respectively. Seedfall was much less 114 m (375 ft) from the edge of the clearcut but was still quite heavy (40,000 to 230,000/ha or 16,000 to 93,000/acre). Sound seed in this study varied from 36 to 76 percent over 2 years. Germination of mountain hemlock seed ranges from 47 to 75 percent *(66)*.

Seedling Development—Mountain hemlock is easily transplanted and propagated by seed and cuttings *(76)*. Heavy seeds germinate more rapidly *(44)*. Germination, which is epigeal, occurs on snow, mineral soil, or organic soil if sufficient moisture is available. Young seedlings grow best in partial shade *(11)*, and early development is often slow. Increasing light intensity and day-length increase seedling height but delay or prevent terminal-bud formation under shelter *(4)*. Stem dissection of trees on the east side of the Oregon Cascades shows that growth to breast height in natural stands is slower on sites thought to have a late-lying snowpack than on warmer sites.

Mountain hemlock is generally slow to regenerate after disturbances such as logging, site preparation, or wildfire. Most burned areas in the mountain hemlock zone on the Olympic Peninsula do not have adequate stocking for commercial forests (600 trees/ha 1,500/acre) even 55 to 88 years after wildfires *(3)*. Reproduction is greater during normal-to-wet growing seasons, than during dry growing seasons, and greater in areas near live trees at the edge of fires and near trees that survive the fires than in areas farther from seed sources. In the parkland subzone, reproduction is limited to the margins of tree clumps *(48,72)*, except when successive years with earlier than normal snowmelt allow invasion of subalpine meadows *(3,23)*.

Young stands 20 to 40 years old (some in burned areas) in southern Oregon and northern California may be pure mountain hemlock and quite dense (9,900 to 24,700 trees/ha, or 4,000 to 10,000/acre) *(11)*.

In Oregon, mountain hemlock forests typically regenerate slowly after they are clearcut. In a study of 25 clearcuts, 5 to 11 years were required to reach 60-percent stocking on 0.0012-ha (0.003-acre) subplots *(56)*. Establishment of seedlings during the first 2 years in an Oregon shelterwood cut was very low because germinants were few at low residual basal areas (less than 11.5 m^2/ha or 50 ft^2/acre) and all seedlings died at all higher basal areas *(69)*.

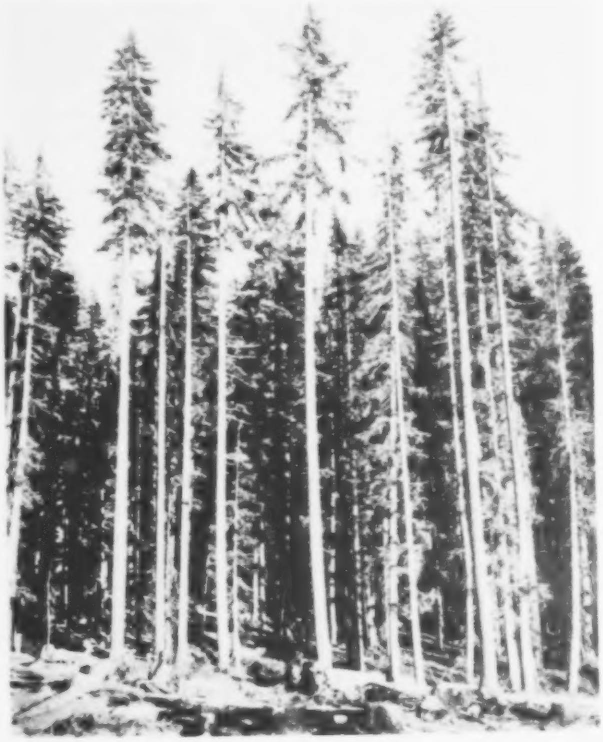

Figure 3—*Forest-grown mountain hemlock, showing good form, pruning, and height.*

The normally slow restocking process is retarded by slash treatment. On the east side of the Cascade Range in Oregon, treated (generally piled and burned) clearcuts had lower stocking (33 percent based on 0.0004-ha (0.001-acre) subplots) than untreated clearcuts (57 percent) because of destruction of advance regeneration and a 50-percent decrease in the number of subplots stocked with natural, postharvest reproduction *(61)*. These clearcuts ranged from 3 to 19 years old. Stocking of mountain hemlock and its associates near Willamette Pass, OR, in 13-year-old strip cuts with unburned slash was 95 percent (on subplots of 0.0012 ha or 0.003 acre), compared with 82 percent in units that had been burned. The difference was due to advance regeneration of silver fir and mountain hemlock in the unburned clearcuts. These studies indicate that stocking in clearcuts in the mountain hemlock zone is typically made up of postharvest naturally seeded trees, such as mountain hemlock, Shasta red fir *(Abies magnifica* var. *shastensis)*, silver fir, lodgepole pine, and western white pine *(Pinus monticola)*; and advance regeneration of mountain hemlock and Shasta red fir *(56,67)*. Planting has been relatively ineffective in speeding regeneration on these cold, snowy sites compared with advance and postharvest natural regeneration that slowly provide adequate to abundant stocking.

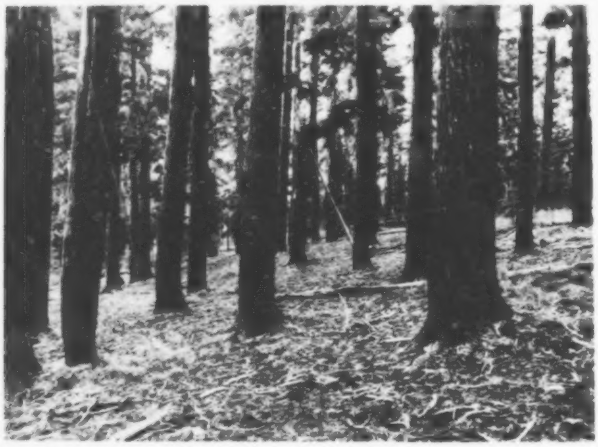

Figure 4—*Well-stocked pure mountain hemlock stand in the central high Cascades of Oregon with canopy trees 300 to 400 years old.*

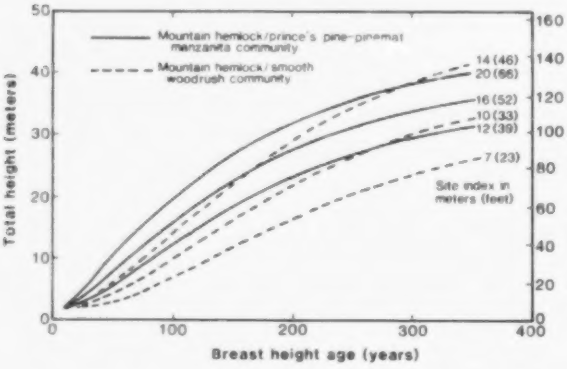

Figure 5—*Height growth curves for two mountain hemlock communities on the east side of the Cascade Range in central Oregon (adapted from* 43*). Mean site index (base age 100 years) and form of height growth curve differ markedly between communities.*

Healthy mountain hemlock saplings (mean d.b.h. 4.5 cm, 1.8 in) respond well to release, in both diameter and height growth *(68)*. Understory saplings with crown ratios greater than 50 percent and growing fastest before release will likely be the best crop trees *(68)*.

Regeneration of mountain hemlock varies in response to environmental gradients. In six strip cuts at Willamette Pass, OR, it decreases from the south (shaded) side to the north (unshaded) side. In the Cascade Range in central Oregon, it decreases with increasing cover of grass and forbs *(67)*. Near Windigo Pass, OR, mountain hemlock makes up an increasing proportion of tree regeneration as elevation and pumice depth increase *(56)* and so becomes increasingly important for reforesting these harsher sites. In Oregon, the proportion of mountain hemlock to other species in clearcuts and burned areas typically is lower than that in surrounding mature stands, whereas the proportion of lodgepole pine, western white pine, and Shasta red fir reproduction is relatively higher.

Seedlings and small saplings of mountain hemlock tolerate heavy snowpacks well. Bent boles and branches spring erect after snowmelt. Leader replacement by axial buds is less frequent than in other North American hemlocks, and the drooping leaders take 3 or more years to become erect *(40)*.

Vegetative Reproduction—Layering is an important method of reproduction on muskegs and krummholz in Alaska but is insignificant in subalpine tree clumps in the north Cascades of Washington *(48)* and in forested areas in general.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature trees range in height from 15 m (50 ft) on poor sites to 46 m (150 ft) on the best sites (figs. 3, 4). Depending on stocking, diameters of old trees range from 30 cm (12 in) on poor sites to 150 cm (60 in) on good sites (fig. 4). The record tree of the American Forestry Association's list of big trees is 34.4 m (113 ft) tall and 224 cm (88 in) in d.b.h. Mountain hemlocks 700 to 800 or more years old are reported in British Columbia *(9)* and at Mount Rainier National Park, WA.

Mountain hemlock grows slowly in height (fig. 5) and in diameter. Three investigators found that stem-dissected trees in Oregon and southern Washington without signs of impeded height growth were only 7 to 28 m (23 to 91 ft) tall at 100 years *(39,43,54)*. Height growth of mountain hemlock is initially slower than that of western hemlock but continues at a moderate rate to greater age. As a result, use of western hemlock site curves in old mountain hemlock stands leads to large overestimates of growth and yield *(39)*.

Site index (base age 100 years) and the form of the height growth curve are different in different plant communities in the central Oregon Cascades (fig. 5) *(43)*. The mountain hemlock/smooth woodrush *(Tsuga mertensiana/Luzula hitchcockii)* and mountain hemlock/prince's-pine-pinemat manzanita *(T. mertensiana/Chimaphila umbellata—Arctostaphylos nevadensis)* communities have ranges in site index of 7 to 14 m (23 to 46 ft) and 13 to 19 m (43 to 62 ft), respectively. In the Coast Mountains of British Columbia, site index (base age 100 years) ranges from less than 6 m (20 ft) on xeric sites to 34 m (110 ft) on the best sites *(46)*.

Mountain hemlock stands at least 200 years old can have high basal areas and volumes; the highest values are in mixed species stands. In the mountain hemlock zone in British Columbia, stands in which that species makes up more than half the volume (59 to 79 percent) have volumes of 125 to 924 m^3/ha (1,786 to 13,204 ft^3/acre); volumes are much higher (range 588 to 1348 m^3/ha, 8,397 to 19,260 ft^3/acre) in stands where mountain hemlock makes up less than half the volume (9 to 36 percent) *(9)*. These more productive mixed-species stands usually grow on deeper soils irrigated by seepage and have a slightly longer average snow-free period, whereas the communities in which mountain hemlock forms a majority of the stocking occupy the poorer, colder sites.

A similar pattern occurs in the Cascade Range in southern Oregon *(42)*. The mountain hemlock/grouse whortleberry community (nearly pure mountain hemlock) produces an estimated 1.0 m^3/ha (14 ft^3/acre) per year, and the Shasta red fir–mountain hemlock/pinemat manzanita/long-stoloned sedge community produces an estimated 3.8 to 9.8 m^3/ha (54 to 140 ft^3/acre) per year *(42)*. The latter community tends to grow on warmer sites, and most of the productivity is by Shasta red fir, not mountain hemlock. Basal areas of both communities are high, 76 and 62 m^2/ha (330 and 270 ft^2/acre), respectively. Mountain hemlock communities in the western Cascades of Oregon and Washington commonly have a mixture of other tree species; estimated productivity ranges from 3.8 to 7.6 m^3/ha (54 to 108 ft^3/acre) per year *(8,38)*. Volume tables are available for mountain hemlock for Alaska *(32)* and the central Oregon Cascades *(6)*. Volume growth, biomass, and leaf area equations are also available *(1,26,71,81,87)*.

Leaf area index (all sides), like volume productivity, is lower in nearly pure mountain hemlock forest (10 m^2/m^2 or 10 ft^2/ft^2) *(25)* than in mixed species forest (35 m^2/m^2 or 35 ft^2/ft^2) *(88)* in the Cascade Range.

Rooting Habit—Mountain hemlock is usually shallow rooted. In British Columbia, roots are mainly confined to the forest floor *(9,45)*. This is not surprising because of the high proportion of soil nutrients in the forest floors of these forests. Mountain hemlock will root adventitiously when, for example, 10 to 20 cm (4 to 8 in) of volcanic tephra is added to the soil surface *(91)*.

Two-thirds to three-quarters of the net primary productivity (NPP) is allocated below ground, according to the available data on three stands 130 to 280 years old dominated by silver fir but with significant mountain hemlock components *(30,84)*. This high allocation below ground is probably caused by the need to obtain sufficient nutrients in these infertile soils *(30)*. Mycorrhizae were found to be important sinks for carbon and components of nutrient cycles in one stand *(84)*.

Reaction to Competition—Mountain hemlock is classed as tolerant of shade and other forms of competition *(10,48,55)* and, based on synecological studies, is more tolerant than all its associates except Pacific silver fir *(46)*, western hemlock, and Alaska-cedar.

Mountain hemlock is considered a minor climax species on most of its habitats; however, it pioneers on glacial moraines in British Columbia and Alaska *(11)* where it is nevertheless considered indicative of the climax forest *(46)*; also see references in *(19)*. Pacific silver fir is a major climax species in many communities of the mountain hemlock forest subzone in British Columbia *(9)* and Washington and northern Oregon *(20)*. Alaska-cedar, western redcedar *(Thuja plicata)*, and western hemlock *(Tsuga heterophylla)*, however, are climax associates on some sites. Mountain hemlock is more commonly the major climax species in the mountain hemlock zone south of central Oregon where Pacific silver fir does not occur.

Mountain hemlock often succeeds lodgepole pine or subalpine fir when these species pioneer on drier sites *(20)*. It also tends to replace Engelmann spruce when the two species occur together, possibly because hemlock is better able to withstand the allelopathic effects of spruce than are other associated species *(76)*.

Damaging Agents—The most striking damage to mountain hemlock is probably that caused by laminated root rot *(Phellinus weiri)* in the high Cascades of central Oregon *(49)*. This fungus spreads from centers of infection along tree roots so that all trees are killed in circular areas that expand radially. Mountain hemlock is the most susceptible tree in these forests *(18,49)*, and *Phellinus* moves faster (34 cm/yr; 13.3 in/yr) through nearly pure mountain hemlock (91 percent hemlock) than through a more heterogeneous conifer (74 percent hemlock) stand (23 cm/yr; 9.1 in/yr) *(49)*. Growth and coalescence of *Phellinus* pockets have produced infected areas of more than 40 ha (100 acres). The low levels of available nitrogen in the forest floor and mineral soil *(51)* stress mountain hemlock, increasing its susceptibility to infection by *Phellinus*, as indicated by a seedling growth chamber study *(52)*.

Seedlings of mountain hemlock and associated species recolonize disease-killed areas immediately behind the advancing mortality front. These seedlings are apparently not susceptible to reinfection by *P. weiri* for 80 to 120 years *(89)*. This may be due to greater vigor caused by higher levels of available nitrogen (up to a 4-fold increase), higher temperatures, and more growing-season moisture in this regrowth zone *(7,89)*.

Other common fungal pests of mountain hemlock include several heart rots *(Heterobasidion annosum, Phellinus pini, Fomitopsis pinicola,* and *Phaeolus schweinitzii) (11,72)*, of which Indian paint fungus *(Echinodontium tinctorum)* is perhaps the most common and damaging *(42)*. Several needle diseases and a snow mold *(Herpotrichia nigra)* also attack mountain hemlock but are not considered serious pests *(11)*.

The mountain hemlock race of hemlock dwarf mistletoe *(Arceuthobium tsugense)* is a potentially damaging parasite that causes witches' broom, reduction in vigor, and occasionally death *(11,50)*. It is found throughout most of the range of mountain hemlock, but reported infection of mountain hemlock decreases from Washington north *(36)*. Dwarf mistletoe rarely infects mountain hemlock in Alaska, though western hemlock is often infected. Several defoliating insects, bark beetles, and wood-boring insects attack mountain hemlock but do not cause extensive damage *(11)*.

Before effective fire suppression, many mountain hemlock stands south of Alaska probably succumbed to fire, as is indicated by the many young stands *(11,20)*. The species is considered susceptible to fire because it often retains branches almost to the ground, grows in clusters, and, in Oregon, often has well-developed forest floors that dry out in the summer *(72)*.

Wind commonly destroys trees in the coastal strip of British Columbia *(45)* and Alaska where fire is not important *(35)*. As cutting is increased in mountain hemlock forests, wind damage will probably become a more common cause of mortality of this shallow-rooted species. Periodic snow breakage may remove 2 to 6.5 percent of the foliage mass *(29)*.

After the eruption of Mount St. Helens and deposition of tephra on foliage and soil (18 cm, 7 in), growth slowed but trees did not die *(41)*.

Special Uses

Perhaps the most important use of mountain hemlock is for watershed protection and the scenic beauty it adds to subalpine landscapes. It is well adapted to produce attractive forest on the more extreme subalpine sites. The Mount Jefferson (fig. 2) and Three Sisters Wildernesses, heavily used year-round recreation areas in Oregon, provide excellent examples. Stands of this species are said to be well suited to the conservation of snow (see references in *19)*. Its slow growth contributes to its attractive, dense foliage and usually balanced form so that it is a desirable ornamental, including the cultivars that make fine dwarf specimens or have silvery foliage *(76)*.

Some mountain hemlock forest types are important deer summer range on Vancouver Island *(34)*. A shrubby plant association (Mountain Hemlock—Copperbush) there provides abundant browse in old stands as well as in early seral conditions, so harvesting does not significantly affect food availability.

Genetics

Mountain hemlock has several morphological characteristics that separate it from most other species of *Tsuga*, including branchlets not all in one plane; needles radially arranged, relatively thick, with stomata on both surfaces; cones generally larger with more scales; and pollen with air bladders. Because of these spruce-like characteristics, the genetic background of mountain hemlock was under some question *(11,13)* until recently. Mountain hemlock was proposed as a hybrid between western hemlock and Sitka spruce *(Picea sitchensis)* by several French taxonomists and assigned to the new genus *Tsugo–Picea* (see references in *11,13*). Recent studies of pollination mechanisms *(59)*, embryology *(61)*, and leaf pigment chemistry *(74)*, however, place the species firmly in the genus *Tsuga*. These studies are consistent with the proposal by Taylor *(74)* that *Picea* and *Tsuga* are closely related genera, and mountain hemlock is more similar to *Picea* than are other *Tsuga* species *(59,74)*.

Individuals morphologically intermediate between western hemlock and mountain hemlock are occasionally found where the two species occupy the same site. These populations have been given hybrid status *(Tsuga × jeffreyi* (Henry) Henry) *(11,13,47)*. A study of leaf pigment chemistry of 43 morphologically intermediate individuals collected from throughout western Washington indicated, however, that only three (all from Corral Pass near Mount Rainier) were chemically intermediate and so were potentially of hybrid origin *(74)*. Six leaf cuticle characteristics of *Tsuga × jeffreyi* in Britain were similar to mountain hemlock and dissimilar to western hemlock *(70)*, also not supporting hybrid status. The limited overlap in the timing of pollen release *(14)* and failure of all known controlled pollinations to produce filled seeds (in British Columbia *(53)* and in Oregon (cited in *74*) support the conclusion that true hybrids are probably much rarer than the morphological intermediates on which hybrid status is based, if such hybrids occur at all.

A California form of mountain hemlock has been given specific status *(Tsuga crassifolia* Flous) and is proposed as a hybrid between Engelmann spruce and mountain hemlock *(13)*. The hybrid swarms expected from backcrosses with the parent taxa have not been observed *(13)*, however, and this specific status and phylogeny are not generally recognized by taxonomists *(17,47,57)*.

All mountain hemlock in the Siskiyou Mountains from the Oregon–California border south were recently given subspecific status as *Tsuga mertensiana* (Bong.) Carr. ssp. *grandicona* Farjon, in recognition of the generally larger cones of trees in this region *(17,63)*. This classification is less ambitious than the new species *T. crassifolia*.

Clausen *(10)* studied the mountain hemlock phenotypes of erect simple stems and prostrate krummholz (elfinwood) over a gradient in elevation (3050 to 3350 m; 10,000 to 11,000 ft) in the Sierra Nevada and described them as genetic races. It has not been determined, however, whether these growth forms have different genotypes or result solely from different environments.

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Glossary

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Acicular foliage—Needle shaped leaves.

Acropetal—Developing upward from the base toward the apex.

Adventitious—Plant organs produced in an unusual or irregular position, or at an unusual time of development.

Aerobic—Capable of living only in the presence of free oxygen.

Afterripening—Enzymatic process occurring in seeds, bulbs, tubers, and fruit after harvesting; often necessary for germination or resumption of growth.

Air layering—Inducing root development on an undetached aerial portion of a plant, commonly by wounding it, treating it with a rooting-stimulant, and wrapping it in moist material under a waterproof covering, so that the portion so treated is capable of independent growth after separation from the mother plant.

All-aged—A condition of a forest or stand that contains trees of all or almost all age classes. It is generally a primary stand where individuals have entered at various times when and where space permitted. (*See* **Uneven-aged**).

Allele—One of an array of genes possible at a certain position (locus) on a given chromosome.

Allelopathy—The influence of plants, other than microorganisms, upon each other, arising from the products of their metabolism.

Allopatric—Occurring in different areas or in isolation. (*Cf.* **Sympatric**).

Alluvial—A type of azonal soil which is highly variable and is classified by texture from fine clay and silt soils through gravel and boulder deposits.

Alluvium—Soil, usually rich in minerals, deposited by water, as in a floodplain.

Alpha pinene—A hydrocarbon of the terpene class occurring in many essential oils; it has a density of about 0.855 and an index of refraction of about 1.465, both at 25° C (77° F).

Anaerobic—Capable of living in the absence of, or not requiring, molecular oxygen.

Andesite—An extrusive usually dark grayish rock consisting essentially of oligoclase or feldspar.

Anemophilous—Normally wind-pollinated.

Anther—The part of the stamen that develops and contains pollen.

Anthesis—The time at which a flower comes into full bloom.

Apophysis—The rounded, exposed thickening on the scales of certain pine cones.

Appalachian Highlands—The lands of the Appalachian Mountains extending from central New York south to northeastern Alabama.

Arbuscula—A small or low shrub having the form of a tree.

Argillite—A compact argillaceous (clayey) rock differing from shale in being cemented by silica and from slate in having no slaty cleavage.

Arillate—Having an aril (an appendage, outgrowth, or outer covering of a seed, growing out from the hilum or funiculus).

Auxin—A natural hormone that regulates plant growth, generally identified with β-indolylacetic acid (IAA), a heteroauxin.

Backcross—A cross between a hybrid and either one of its parents.

Basalt—A dark gray to black colored, dense to fine-grained igneous rock.

Basipetal—Developing toward the base from the apex.

Batture—Land between the river and the manmade levees that border it.

Berry—A simple, pulpy fruit of a few or many seeds (but no stones) developed from a single ovary.

Beta phellandrene—A terpene with a density of about 0.84 and an index of refraction of about 1.48, both at 25° C (77° F).

Beta pinene—A terpene with a density of about 0.867 and an index of refraction of about 1.477, both at 25° C (77° F).

Biomass—The total quantity, at a given time, of living organisms of one or more species usually expressed in weight per unit area.

Bisexual—Having both male and female sexual reproductive structures.

Bonsai—The culture of miniature potted trees, which are dwarfed by stem and root pruning and controlled nutrition.

Boreal forest—A coniferous forest of the northern hemisphere characterized by evergreen conifers such as spruce, fir, and pine.

Breast height—1.37 m or 4.5 ft above groundline on standing trees, a standard height in USA for recording diameter, girth, or basal area.

Campanulate—Bell-shaped.

Canadian Shield—The Precambrian nuclear mass centered in Hudson Bay around which, and to some extent upon which, the younger sedimentary rocks have been deposited.

Canopy—The more or less continuous cover of branches and foliage formed collectively by the crowns of adjacent trees.

Capsule—A dry usually many-seeded fruit composed of two or more fused carpels that split at maturity to release their seeds.

Carr—A deciduous woodland on a permanently wet, organic soil.

Catena—A sequence of different soils, generally derived from similar parent soil material, each of which owes its character to its peculiar physiographic position.

Catkin—A drooping elongated cluster of bracted unisexual flowers found only in woody plants.

Chromosome—A microscopic, usually rod-like body carrying the genes. Number, size, and form of chromosomes are usually constant for each species.

Cirque—A deep, steep-walled basin shaped like a half bowl, on a mountain.

Clearcut—The cutting method that describes the silvicultural system in which the old crop is cleared over a considerable area at one time. Regeneration then occurs from (a) natural seeding from adjacent stands, (b) seed contained in the slash or logging debris, (c) advance growth, or (d) planting or direct seeding. An even-aged forest usually results.

Cleft graft—The stock is cut off, split, and then one or more scions are placed in this cleft (split) making the cambium layers of the stock and scion match.

Climax community—The terminal stage of an ecological succession sequence which remains relatively unchanged as long as climatic and physiographic factors remain stable.

Clinal—Sloping.

Clone—Any plant propagated vegetatively and therefore considered a genetic duplicate of its parent.

Codominant (a crown class)—Species in a mixed crop that are about equally numerous and vigorous; forming part of the upper canopy of a forest, less free to grow than dominants but freer than intermediate and suppressed trees.

Collenchyma—Flexible, supportive plant tissue usually of elongated living cells with unevenly thickened walls which are usually interpreted as primary walls.

Colluvium—Rock detritrus and soil accumulated at the foot of a slope.

Conglomerate—Made up of parts from various sources or of various kinds.

Corymb—A flat-topped floral cluster with outer flowers opening first.

Cotyledon—An embryonic leaf, which often stores food materials, characteristic of seed plants.

Crown class—Any class into which trees of a stand may be divided based on both their crown development and crown position relative to crowns of adjacent trees. The four classes commonly recognized are dominant, codominant, intermediate, and suppressed.

Culmination of mean annual increment—For a tree or stand of trees, the age at which the average annual increment is greatest. It coincides precisely with the age at which the current annual increment equals the mean annual increment of the stand and thereby defines the rotation of a fully stocked stand that yields the maximum volume growth.

Cultivar—A contraction of "cultivated variety." It refers to a plant type within a particular cultivated species that is distinguished by 1 or more characters.

Current annual increment (CAI)—The amount by which the volume of a tree or stand increases in 1 year.

Cymose—Bearing a cyme, a more or less flat-topped floral cluster with the central flowers opening first.

Cytokinins—A class of hormones that promote and control growth responses of plants.

Dehisce—To split open when ripe, usually along definite lines or sutures to release seeds.

Deliquescent branching—A mode of branching in trees in which the trunk divides into many branches leaving no central axis, as in elms. (*See* **Excurrent branching.**)

Destructive distillation—The decomposition of wood by heating out of contact with air, producing primarily charcoal.

Diallel cross—Complete: a mating design and subsequent progeny test resulting from the crossing of n parents in all possible n^2 combinations including selfs and reciprocals. Incomplete: a partial sampling—any individual family or type of family may be omitted. In either type of cross, identities of both seed and pollen parents are maintained for each family.

Dichogamy—In a perfect flower, maturation of stamens and pistils occurs at different times, thus preventing self-pollination.

Dioecious—Having staminate (male) flowers and pistillate (female) flowers on different plants of the same species.

Diorite—A granular crystalline igneous rock commonly of acid plagioclase and hornblende, pyroxene, or biotite.

Diploid—An organism which has two sets of chromosomes in its cells, paternal and maternal.

Disclimax—A relatively stable ecological community often including kinds of organisms foreign to the region and replacing the climax because of disturbance.

DNA—Deoxyribonucleic acid, the carrier of genetic information (genes) in cells.

Dominant (a crown class)—One of four main crown classes recognized, on a basis of relative status and condition in the crop. Dominant trees have their crowns in the uppermost layers of the canopy and are largely free-growing.

Duff—The partially decomposed organic matter (litter of leaves, flowers, and fruits) found beneath plants, as on a forest floor.

Ecotone—Any zone of intergradation or interfingering, narrow or broad, between contiguous plant communities.

Ecotype—A subgroup within a species, which is genetically adapted to a habitat type that is different from the habitat type of other subgroups of that species. It normally has a large geographical distribution.

Ectotrophic mycorrhiza (ectomycorrhiza)—A mycorrhiza growing in a close web on the surface of an associated root; generally formed by basidiomycete fungi.

Edaphic—Pertaining to the soil in its ecological relationships.

Endocarp—The innermost differentiated layer of the pericarp, or fruit wall, as in the stoney part of a drupe.

Endosperm—A nutritive tissue in seed plants formed within the embryo sac.

Endotrophic mycorrhiza (endomycorrhiza)—A mycorrhiza penetrating into the associated root and ramifying between the cells; generally formed by phycomycete fungi.

Epicotyl—The portion of the axis of an embryo or young seedling above the point where the cotyledon(s) is attached.

Epigeal—The part of the seedling above the cotyledon(s). *(Cf.* **Hypogeal).**

Epiphyte—An organism that grows on another plant but is not parasitic on it.

Even-aged management—The application of a combination of actions that results in the creation of stands in which trees of essentially the same age grow together. The difference in age between trees forming the main canopy level of a stand usually does not exceed 20 percent of the age of the level of a stand at maturity. Regeneration in a particular stand is obtained during a short period at or near the time that a stand has reached the desired age or size for regeneration, and is harvested. Cutting methods producing even-aged stands are clearcut, shelterwood, or seed tree.

Exalbuminous—Descriptive of seeds that lack endosperm.

Excurrent branching—Tree growth in which the main axis continues to the top of the tree from which smaller, lateral branches arise (as in conifers). (*See* **Deliquescent branching.**)

Fastigiate form—Strictly erect and more or less parallel vertical branches.

Fbm—Foot (feet) board measure (board foot [feet]).

Fen—A bog with springs as a water source other than precipitation.

Feral goats—Goats that have escaped from domestication and become wild.

Fluvial—Produced by stream action.

Frost rings—A zone of injured cambium tissue caused by frost.

Funiculus—The basal stalk of an ovule arising from the placenta in the angiosperms.

Gabbro—A dark, coarse-textured, heavy rock composed of calcium feldspar and augite with a small amount of quartz.

Gene—The smallest transmittable unit of genetic material consistently associated with a single primary genetic effect.

Genet—A single sexually produced individual.

Germinative capacity—Percentage of seeds that germinate during the normal period of germination.

Germplasm—Within an individual or group the collective materials that are the physical basis for inheritance.

Gibberellin—A plant hormone useful in regulating the growth characteristics of many plants.

Glade—An open space in a forest.

Gneiss—A metamorphic rock derived from either igneous or sedimentary formations.

Graft incompatibility—Said of plants which, when grafted together, fail to form a lasting union.

Granite—A very hard natural igneous rock formation.

Grood soils—Nut-structured soils characteristic of the transition zone between prairie soils and podzolic soils, i.e., prairie-forest soils.

Group selection—The cutting method which describes the silvicultural system in which trees are removed periodically in small groups resulting in openings that do not exceed 0.4 to 0.8 hectare (1 to 2 acres) in size. This leads to the formation of an uneven-aged stand in the form of a mosaic of age-class groups in the same forest.

Growing stock level (GSL)—A numerical index. The residual square meters of basal area per hectare (square feet of basal area per acre) when the average stand diameter is 25 cm (10 in) or more in d.b.h. Basal area retained in a stand with an average d.b.h. of less than 25 cm (10 in) is less than the designated level.

Haploid—An organism with one basic chromosome set symbolized by *n*.

Harden-off—The process of gradually reducing the amount of water and lowering the temperature for plants in order to toughen their tissues, making it possible for them to withstand unfavorable (usually cold) environmental conditions.

Hedging—Close-cropping.

Heptane—Any of several isometric hydrocarbons of the methane series.

Hermaphrodite (bisexual)—A flower with both functional male and female reproductive organs.

Heterozygote—An organism whose cells have one or more sets of unlike alleles.

High-lining—The underside of a forest canopy that is uniformly cropped by deer at the highest level they can browse. A browseline.

Hilum—The scar on a seed marking the point of attachment of the ovule.

Hybrid swarm—An extremely variable population derived from the hybridization of two different taxa and consisting of the products of subsequent segregation and recombination, backcrossing, and crossing between the hybrids themselves. It occurs where the range of inter-fertile species overlap.

Hydroponics—The cultivation of plants, without soil, in water solutions of nutrients required for growth.

Hydrosere—An ecological sere (plant community) originating in an aquatic habitat.

Hypanthium—A floral tube formed by the fusion of the basal portions of the sepals, petals, and stamens, and from which the rest of the floral parts emanate.

Hypocotyl—The part of an embryo or seedling below the cotyledon(s) and above the radicle (but sometimes including it).

Hypogeal—Describes seed germination in which the colytedons remain beneath the surface of the soil. (*Cf.* **Epigeal**).

Hypogeous—Growing or developing below the soil surface.

Igneous rock—Formed by solidification of molten magma.

Imperfect flower—A flower which lacks either stamens or carpels.

Inbreeding—In plants, a breeding system in which sexual reproduction involves the interbreeding of closely related plants by self-pollination or backcrossing.

Individual tree selection—The cutting method that describes the silvicultural system in which trees are removed individually, here and there, each year over an entire forest or stand. The resultant stand usually regenerates naturally and becomes all-aged.

Indolebutyric acid (IBA)—A synthetic auxin widely used in horticulture to induce rooting of cuttings.

Inland Empire—A region in eastern Washington, northern Idaho, and western Montana, named for commercial purposes.

Intergeneric—Existing or occurring between genera.

Intermediate (a crown class)—A tree of the middle canopy dominated by others in the dominant and codominant crown classes.

Intermountain—In the Forest Service, an area that includes the States of Montana, Idaho, Utah, Nevada, and the western quarter of Wyoming.

Intraspecific—Refers to some relationship between the members of the same population or species.

Introgression—The entry or introduction of a gene from one gene complex to another.

Isoline—Isogram; a line on a map or chart along which there is constant value (temperature, pressure, or rainfall).

Isozymes (isoenzymes)—Any two or more chemically distinct but functionally like enzymes.

Jackstrawed fuel—Trees that have fallen in tangled heaps.

Juvenile cuttings—The youngest parts of the branches are severed from the plant and rooted to produce new plants.

Karyotype—The character of the chromosomes as defined by their size, shape, and number.

Knee—An abrupt bend in a stem or tree trunk, or an outgrowth rising from the roots of some swamp-growing trees such as baldcypress.

Krummholz—The stunted growth habit, literally crooked wood, caused by wind and found in certain tree species at their upper limit of distribution.

Cushion krummholz—Alpine trees exposed to severe wind conditions are wind-pruned to a cushion-like mat.

Flagged krummholz—The tallest trees protrude from the protective snow pack and become wind-battered "flags."

Lacustrine—Related to or growing in lakes.

Lake Agassiz Basin—A late glacial and early post-glacial lake area in southern North Dakota and western Minnesota.

Lake States—Those States bordering the Great Lakes, that is, Minnesota, Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York.

Lammas—The part of an annual shoot that is formed after a summer pause in growth.

Layering—The rooting of an undetached branch, laying on or partially buried in the soil, which is capable of independent growth after separation from the mother plant.

Leaf area index (LAI)—Leaf surface area per unit of land surface area. For broad-leaf forests, the index is calculated using only one side of the leaf blade; for needle-leaf stands the total leaf surface is used; and, for mixed broad- and needle-leafed stands, a combination of the two is used.

Lightwood (fatwood, lightered wood or stumps, stumpwood)—Coniferous wood having an abnormally high content of resin and therefore easily set alight (afire).

Lignotubers—A woody swelling at ground level originating from the axils of the cotyledons from whose concealed dormant buds a new tree can develop if the old one is injured. Characteristic of many Eucalypts.

Limonene—A component of pine turpentine with a density of approximately 0.84 and an index of refraction of about 1.47, both at 25° C (77° F).

Litter—The uppermost layer of organic debris on a forest floor consisting essentially of freshly fallen or only slightly decomposed vegetable matter, mainly foliage but also bark, twigs, flowers, and fruits. The L-layer of the organic portion of the soil profile.

Loess—A uniform and unstratified fine sand or silt (rarely clay) deposit transported by wind (an aeolian soil). It is sometimes described as rock flour.

Lumen—Either the cell cavity or a unit of luminous flux equal to the light emitted by a uniform point source of one candle intensity.

Lye—A strong alkaline solution of sodium hydroxide, potassium hydroxide, or the leachate of wood ashes that is rich in potassium carbonate.

Maceration—The process of removing the fleshy tissue surrounding seeds, often by soaking in water.

Macronutrients—The nutritional elements, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur, essential for normal plant growth, development, and reproduction. They are usually derived from the soil.

Mean annual increment (M.A.I. or m.a.i.)—The total increment of trees in a stand up to a given age, divided by that age, usually expressed in annual cubic meters of growth per hectare (cubic feet of growth per acre).

Megagametophyte—The female gametophyte which develops from the megaspore and produces the female gamete(s).

Megasporangium—The sporangium in which megapores are produced; the nucellus of seed plants.

Megaspore—In plants having two types of haploid spores (microspores (male) and megaspores (female)), megaspores give rise to megagametophytes.

Meiosis—Reduction division resulting in the production of haploid gametes; a process consisting of two specialized nuclear divisions ultimately leading to the formation of eggs or sperm.

Meristem—Tissue primarily associated with protoplasmic synthesis and formation of new cells by division.

Mesic—Characterized by intermediate moisture conditions, neither decidedly wet nor decidedly dry.

Mesophyte—A plant whose normal habitat is neither very wet nor very dry.

Mesozoic—An era of geologic history marked by the cycads, evergreen trees, dinosaurs, marine and flying reptiles, and ganoid fishes.

Metamorphism—A pronounced change effected by pressure, heat, and water that results in a more compact and more highly crystalline condition.

Micronutrients (trace elements)—Nutritional elements necessary in minute quantities for normal plant growth, such as boron and manganese.

Micropyle—A minute opening in the integument of an ovule through which the pollen tube normally passes to reach the embryo sac, usually closed in the mature seed to form a superficial scar.

Microsporangium—In plants having two types of haploid spores (microspores and megaspores), the saclike structure in which microspores are produced.

Microspore—A haploid spore produced by meiosis of the microsporocyte and developing into the male gametophyte. The pollen grain of seed plants.

Mine spoil—Earth and rock excavated from a mine.

Mitosis—Normal division of a nucleus into two identical daughter nuclei by a process of duplication and separation of chromosomes.

Monadnock—A hill or mountain of resistant rock surmounting land of considerable area and slight relief shaped by erosion.

Monoecious—Having staminate and pistillate flowers in separate places on the same plant.

Montane—The biogeographic zone made up of relatively moist cool upland slopes below timberline that is characterized by large evergreen trees as a dominant life form.

Mor—A layer of organic material made up of largely unrecognizable plant debris and their decomposition products overlain by litter and lying on the surface of, and essentially unmixed with, the mineral soil. Earthworms are absent.

Muck—Highly decomposed organic material formed under conditions of waterlogging, with few recognizable remains of the original plants.

Mull—A soil whose upper mineral layer has become intimately mixed (mainly through the action of earthworms) with amorphous organic material, sometimes to a depth of 1.2 to 1.5 meters (4 to 5 feet).

Mycelium—The mass of threadlike filaments constituting the vegetative body of a fungus.

Natural pruning (self pruning)—The freeing of the stem of a standing tree of its branches by natural death, disintegration, and/or fall, from such causes as decay, or deficiency of light or water, or snow, ice, and wind breakage.

Naval stores—The products of the resin industry. In the United States they are turpentine, rosin, pine tars, and pitch. Gum naval stores refer specifically to gum turpentine and gum rosin; wood naval stores to wood turpentine and wood rosin.

Normal yield table—A table showing, for one or more species in a fully stocked stand, the growth pattern of a managed even-aged stand derived from measurements at regular intervals covering its useful life. It includes mean d.b.h. and height, number of stems, and standing volume per unit area. The table may also contain a variety of other useful data.

North Central—In the Forest Service, an area that includes Indiana, Illinois, Michigan, Wisconsin, Minnesota, Iowa, and Missouri.

Northeastern—In the Forest Service, an area that includes the New England States plus New York, New Jersey, Delaware, Maryland, Pennsylvania, Ohio, West Virginia, and Kentucky.

Nucellus—The tissue of an ovule, in which the female gametophyte (embryo sac) develops; the megasporangium.

Old growth—Stands of forest trees of either seral or climax species growing singly or in association with other tree species. The stands are usually well past the age of maturity as defined by the culmination of mean annual increment and often exhibit characteristics of decadence. These characteristics may include, but are not limited to: low growth rates, dead and dying trees, snags, and down woody material. The stands are usually characterized by large diameter trees relative to species and site potential, multi-layered canopies, a range in tree diameter sizes, and the presence of understory vegetation. The specific attributes of an old-growth stand are primarily dependent on plant associations and forest cover type.

Oleoresin—The nonaqueous secretion of resin acids dissolved in a terpene hydrocarbon oil which is produced in, or exuded from, the intercellular resin ducts of a living tree or accumulated, together with oxidation products, in the dead wood of weathered limbs or stumps. Commonly called pine gum, gum, pitch, or even sap.

Open-grown—In reference to trees, grown in the absence of woody competition.

Operculum—A caplike structure composed of fused sepals and petals that suggests a lid

Organic soils layers

L-layer—Freshly fallen or only slightly decomposed leaves, twigs, flowers, fruit, and bark lying on the soil surface.

F-layer—Zone of active organic matter fermentation.

H-layer—Humidified zone. The more or less stable fraction from the decomposed soil organic material. Generally, it is amorphous, colloidal, and dark colored.

Ortet—An original plant from which a vegetatively propagated clone has been derived.

Overstory—That portion of the trees in a forest of more than one story forming the upper or uppermost canopy layer.

Ovulate—Bearing or possessing ovules.

Pacific Northwest—In the Forest Service, an area that includes the States of Washington and Oregon.

Pacific Southwest—In the Forest Service, the States of California, and Hawaii plus Guam and the Trust Territories of the Pacific Islands.

Parthenocarpy—The development of fruit without viable seed. It may be induced artificially, as by some foreign pollen, or with hormones.

Peat—Undecomposed or only slightly decomposed organic matter accumulated under conditions of excess moisture. Plant residues show little, if any, morphological change.

Peduncle—A stalk bearing a flower, flower cluster, or a fructification.

Perfect flower—A flower having both stamens and carpels; may or may not have a perianth.

Perianth—A collective term for the floral envelopes, usually the combined calyx and corolla, or tepals of a flower.

Pericarp—The wall of a ripened ovary (fruit) that is homogeneous in some genera and in others is composed of three distinct layers, exocarp, mesocarp, and endocarp.

Permafrost—Permanently frozen ground; generally refers to a layer at some depth below the soil surface. Any layer above it, which thaws in summer, is termed the active layer.

Phenotype—The plant as observed; the product of the interaction of the genes of an organism (genotype) with the environment.

Photoperiodism—The physiological response of an organism to the periodicity and duration of light and darkness which affects many processes including growth, flowering, and germination.

Phyllodes—A flat expanded petiole that replaces the blade of a foliage leaf and which functions in photosynthesis.

Pioneer—A plant capable of invading a newly exposed soil surface and persisting there until supplanted by successor species.

Pistil—Ovule-bearing organ of an angiosperm composed of ovary, style, and stigma. Collectively the pistils are called the genoecium.

Pistillate—Having only female organs. May apply to individual flowers or inflorescences, or to plants of a dioecious species in angiosperms.

Ploidy—Degree of repetition of the basic number of chromosomes.

Plus-tree—A phenotype judged, but not proven by test, to be unusually superior in some quality or qualities.

Podzol—A soil characterized by a superficial layer of raw humus above a generally grey A horizon of mineral soil depleted of sesquioxides of iron and aluminum and of colloids and overlying a B horizon wherein organic matter and/or sesquioxides of iron have accumulated.

Pole-size—A young tree with a d.b.h. of not less than 10.2 cm (4 in). A small pole has a maximum d.b.h. of 20.3 cm (8 in), and a large pole has a maximum d.b.h. of 30.5 cm (12 in).

Polygamo-dioecious—Bearing perfect and pistillate flowers on female trees and only staminate flowers on male trees.

Polygamous—Plants bearing both perfect and imperfect flowers.

Polymorph—One of several forms of an organism.

Primordium—An organ, a cell, or an organized series of cells in their earliest stage of differentiation, e.g., leaf primordium, sclereid primordium, vessel primordium.

Proembryo—Embryo in early stages of development, often the stages before the main body and suspensor become distinct.

Propagule—A plant part such as a bud, tuber, root, or shoot used to reproduce (propagate) an individual plant vegetatively.

Protandry—The termination of shedding of pollen by a flower prior to the stigma of the same flower being receptive.

Proteranthous—Having flowers appearing before the leaves.

Protogyny—The termination of receptivity prior to the maturation of pollen on the same plant or flower.

Provenance—The original geographic source of seed, pollen, or propagules.

Pumice—A volcanic glass full of cavities and very light in weight.

Pyrene—The pit or seed of a drupe which is surrounded by a bony endocarp.

Pyric—Resulting from, induced by, or associated with burning.

Ramet—An individual member of a clone, derived from an ortet.

Receptivity—The condition of the female flower that permits effective pollination.

Rocky Mountains—In the Forest Service, an area that includes the Dakotas, Nebraska, Kansas, Oklahoma, and Texas west of the 100th meridian, New Mexico, Arizona, Colorado, and the eastern three-quarters of Wyoming.

Saddle—A ridge connecting two higher elevations.

Samara—A dry, indehiscent, winged fruit, one-seeded as in *Fraxinus* and *Ulmus* or two-seeded as in *Acer*.

Sapling—A tree more than 0.9 m (3 ft) in height and less than 10.2 cm (4 in) in d.b.h.

Savannah—Essentially lowland tropical and subtropical grassland, generally with a scattering of trees and/or shrubs. If woody growth is absent it is termed a grass savannah; with shrubs and no trees, a shrub savannah; or with shrubs and widely irregularly scattered trees, a tree savannah.

Scarification (for seed)—Pregerminative treatment to make seed coats permeable to water and gases; accomplished usually by mechanical abrasion or by soaking seeds briefly in a strong acid or other chemical solution.

Schist—A metamorphic crystalline rock having a closely foliated structure divisible along approximately parallel planes.

Scion—An aerial plant part, often a branchlet, that is grafted onto the root-bearing part of another plant.

Sclerenchyma—A protective or supporting tissue in higher plants composed of cells with walls thickened and lignified and often mineralized.

Sedimentary—Formed by or from deposits of sediment.

Seed coat (testa)—The outer coat of the seed derived from the integument(s).

Seedling—A tree grown from seed that has not yet reached a height of 0.9 m (3 ft) or exceeded 5.1 cm (2 in) in d.b.h., which would qualify it as a sapling.

Seed tree—The cutting method that describes the silvicultural system in which the dominant feature is the removal of all trees except for a small number of seed bearers left singly or in small groups, usually 20 to 25 per hectare (8 to 10 per acre). The seed trees are generally harvested when regeneration is established. An even-age stand results.

Selection—*See* **Group selection** and **Individual tree selection.**

Self-pruning—*See* **Natural pruning.**

Selfing (self pollination)—The pollination of an individual or biotype with its own pollen, the offspring being termed selfs.

Sere—A sequence of plant communities that successively follow one another in the same habitat from the pioneer stage to a mesic climax.

Serotinous—Late in developing; particularly applied to plants that flower or fruit late in the season and to fruit and cones that remain closed for a year or more after the seeds mature, but also to bud opening, leaf shedding, etc.

Serpentine—A mineral or rock consisting essentially of a hydrous magnesium silicate. It usually has a dull green color and often a mottled appearance.

Serpentinite—A rock consisting almost wholly of serpentine minerals derived from the alteration of previously existing divine and pyroxene.

Sessile—Without a stalk; sitting directly on its base.

Shade-tolerance classes—Very intolerant, intolerant, intermediate, tolerant, very tolerant.

Shelterwood—The cutting method that describes the silvicultural system in which, in order to provide a source of seed and/or protection for regeneration, the old crop (the shelterwood) is removed in two or more successive shelterwood cuttings. The first cutting is ordinarily the seed cutting, though it may be preceded by a preparatory cutting, and the last is the final cutting. Any intervening cutting is termed a removal cutting. An even-age stand results.

Sialic—Light rock rich in silica and alumina, and typical of the outer layer of the earth.

Silvicultural system—A process whereby forests are tended, harvested, and replaced, resulting in a forest of distinctive form. Systems are classified according to the method of carrying out the fellings that remove the mature crop with a view to regeneration and according to the type of forest thereby produced. These are individual tree selection, group selection, shelterwood, seed tree, and clearcut.

Site class—A measure of the relative productive capacity of a site based upon the volume or height (dominant, codominate, or mean) or the maximum mean annual increment of a stand that is attained or attainable at a given age.

Site index (SI)—A measure of site class based upon the height of the dominant trees in a stand at an arbitrarily chosen age, most commonly at 50 years in the East and 100 years in the West.

Skep—A woven straw beehive.

Soil orders—The 10 soil orders used by the Soil Conservation Service of the USDA in their basic system of soil classification are: Alfisol, Aridisol, Entisol, Histosol, Inceptisol, Mollisol, Oxisol, Spodosol, Ultisol, and Vertisol.

Solum—The upper and most weathered part of the soil profile, i.e., the A and B horizons.

Southeastern—In the Forest Service, an area that includes Virginia, the Carolinas, Georgia, and Florida.

Southern—In the Forest Service, an area that includes Alabama, Tennessee, Mississippi, Arkansas, Louisiana, and Oklahoma and Texas east of the 100th meridian.

Southern pines—Within the United States, the 10 species of hard pines with major portions of their ranges below the Mason-Dixon line, i.e., longleaf, shortleaf, slash, loblolly, spruce, Virginia, sand, pitch, Table Mountain, and pond pine.

Sporangium—A hollow, unicellular or multicellular saclike spore-producing structure.

Sporophyll—A modified leaf or leaflike structure which bears sporangia, e.g., the stamens and carpels of the angiosperms.

Staminate—Having pollen-bearing organs (stamens) only. May apply to individual male plants of a dioecious species or to flowers, inflorescences, or strobili.

Stand density—A measure of the degree of crowding of trees within stocked areas, commonly expressed by various growing-space ratios such as crown length to tree height, crown diameter to diameter at breast height (1.37 m or 4.5 ft above the ground) (d.b.h.); crown diameter to tree height; or of stem (triangular) spacing to tree height.

Stemflow—Precipitation that is intercepted by vegetative cover and runs down the stem or major axes of such cover.

Steppe—Arid land with xerophilous vegetation usually found in regions of extreme temperature range and loess soil.

Stereome—A collective physiological term for all supporting tissues in a plant, such as sclerenchyma and collenchyma.

Sterigma—A peg-shaped projection to which the leaves of some conifers (as spruces) are attached on the twigs.

Stigma—The part of the pistil, usually the tip, often sticky, which receives the pollen and upon which the pollen germinates.

Stipe—A supporting stalk, such as the stalk of a pistil, a gill fungus, or the petiole of a fern leaf.

Stipule—A small structure or appendage found at the base of some leaf petioles, usually present in pairs. They are morphologically variable and appear as scales, spines, glands, or leaflike structures.

Stoma—A pore in the epidermis and the two guard cells surrounding it. Sometimes applied only to the pore.

Stool—A living stump capable of producing sprouts.

Stratification—A pregerminative treatment to break dormancy in seeds and to promote rapid uniform germination accomplished by exposing seeds for a specified time to moisture at near-freezing temperature sometimes with a preceding exposure to moisture at room temperature.

Strobilus—The male or female fruiting body of the gymnosperms.

Style—The stalk of a pistil which connects the stigma with the ovary.

Suppressed (a crown class)—Very slowly growing trees with crowns in the lower layer of the canopy and leading shoots not free. Such trees are subordinate to dominants, codominants, and intermediates in the crown canopy.

Sympatric—Species or populations inhabiting the same or overlapping areas. *Cf.* **Allopatric.**

Sympodial—A branching growth pattern in which the main axis is formed by a series of successive secondary axes, each of which represents one fork of a dichotomy.

Taungya method—The raising of a forest crop in conjunction with a temporary agricultural crop.

Taxon—Any formal taxonomic group such as genus, species, or variety.

Tepal—Perianth parts undifferentiated into distinct sepals and petals.

Terpene—Any of various isometric hydrocarbons found especially in essential oils (as from conifers), resins, and balsams.

Testa—The outer coat of the seed derived from the integument(s).

Tetraploid (polyploid)—A cell, tissue, or organism having four sets of chromosomes.

Thermic soil temperature—The mean annual soil temperature is 15° C (59° F) or higher but lower than 22° C (72° C), and the difference between mean summer and mean winter soil temperature is more than 5° C (9° F) at a depth of 50 cm (20 in).

Throughfall—All the precipitation reaching the forest floor minus the stemflow, i.e., canopy drip plus direct precipitation.

Top-to-root ratio or root-to-shoot ratio—The relative weights or volumes of the epicotyl and the hypocotyl of a tree seedling, expressed as a ratio.

Tracheid—An elongated, thick-walled, nonliving conducting and supporting cell found in the xylem of most vascular plants.

Triploid—A cell, tissue, or organism having three sets of chromosomes.

T.S.I. (timber stand improvement)—A loose term comprising all intermediate treatments made to improve the composition, constitution, condition, and increment of a timber stand.

Tuff—A rock composed of the finer kinds of volcanic detritus usually fused together by heat.

Umbo—A blunt or rounded projection arising from a surface, as on a pine cone scale.

Uneven-aged—A condition of forest or stand that contains intermingled trees that differ markedly in age. By convention, a minimum range of 10 to 20 years is generally accepted, though with rotations of not less than 100 years, 25 percent (USA) of the rotation may be the minimum.

Variety—A subdivision of a species, usually separated geographically from the typical, having one or more heritable, morphological characteristics which differ from the typical even when grown under the same environmental conditions; a morphological variant.

Xerophyte—A plant that is adapted to dry or arid habitats.

Summary of Tree Characteristics

Russell M. Burns and Barbara H. Honkala[1]

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	**Scientific name**				
Ailanthus	*Ailanthus altissima* (Mill.) Swingle	Intolerant	D	E	U, I, E
Alaska-cedar	*Chamaecyparis nootkatensis* (D. Don) Spach	Tolerant	M	E	H, S
Alpine larch	*Larix lyallii* Parl.	Very intolerant	M	E	E, I
American basswood	*Tilia americana* L.	Tolerant	Perfect	E	AL, I, S
American beech	*Fagus grandifolia* Ehrh.	Very tolerant	M	E	AL, O, S
American elm	*Ulmus americana* L.	Intermediate	Perfect	E	AL, I, M, U
American holly	*Ilex opaca* Ait.	Very tolerant	D	E	I, U
American hornbeam	*Carpinus caroliniana* Walt.	Very tolerant	M	E	AL, U, I, E, S, H, M
Atlantic white-cedar	*Chamaecyparis thyoides* (L.) B.S.P.	Intermediate	M	E	S, H
Ausubo	*Manilkara bidentata* (A. DC.) Chev.	Very tolerant	Perfect	E	I, O
Baldcypress	*Taxodium distichum* (L.) Rich. var. *distichum*	Intermediate	M	E	S, U, I, AL, E
Balsam fir	*Abies balsamea* (L.) Mill.	Very tolerant	M	E	S, I, H
Balsam poplar	*Populus balsamifera* L.	Very intolerant	D	E	I, E
Bigcone Douglas-fir	*Pseudotsuga macrocarpa* (Vasey) Mayr	Intolerant	M	E	I, AL
Bigleaf maple	*Acer macrophyllum* Pursh	Very tolerant	Polygamous	E	I, U, S, M, E, AL
Bigtooth aspen	*Populus grandidentata* Michx.	Very intolerant	D	E	S, AL, I
Bitternut hickory	*Carya cordiformis* (Wangenh.) K. Koch	Intolerant	M	H	U, I, M, AL
Black ash	*Fraxinus nigra* Marsh.	Intolerant	Polygamous	E	H, E
Black cherry	*Prunus serotina* Ehrh.	Intolerant	Perfect	H	I, U, AL
Black cottonwood	*Populus trichocarpa* Torr. & Gray	Very intolerant	D	E	E, I
Black locust	*Robinia pseudoacacia* L.	Very intolerant	Perfect	E	I, U, AL
Black maple	*Acer nigrum* Michx. f.	Very intolerant	Polygamous	E	M, I, E, S
Black oak	*Quercus velutina* Lam.	Intermediate	M	H	S, AL, M, U, E, I
Black spruce	*Picea mariana* (Mill.) B.S.P.	Tolerant	M	E	H, S, I, E
Black tupelo	*Nyssa sylvatica* Marsh. var. *sylvatica*	Tolerant	Plygamo-D	E	U
Black walnut	*Juglans nigra* L.	Intolerant	M	H	AL, E
Black willow	*Salix nigra* Marsh.	Very intolerant	D	E	E
Blue oak	*Quercus douglasii* Hook. & Arn.	Intolerant	M	H	AL, I, M
Blue spruce	*Picea pungens* Engelm.	Intermediate	M	E	M, H, I
Bluegum eucalyptus	*Eucalyptus globulus* Labill.	Intolerant	Perfect	E	U, AL, I, AR
Boxelder	*Acer negundo* L.	Tolerant	D	E	E, I, AL, U, M
Brewer spruce	*Picea breweriana* Wats.	Tolerant	M	E	E
Bur oak	*Quercus macrocarpa* Michx.	Intermediate	M	H	AL, M, S
Butternut	*Juglans cinerea* L.	Intolerant	M	H	AL, E
Cabbage palmetto	*Sabal palmetto* (Walt.) Lodd. ex J. A. & J. H. Schult.	Tolerant	Perfect	H	E, AL, U, S
California black oak	*Quercus kelloggii* Newb.	Intolerant	M	H	AL, I, M
California-laurel	*Umbellularia californica* (Hook. & Arn.) Nutt.	Tolerant	Perfect	H	I, M, U
California red fir	*Abies magnifica* A. Murr.	Tolerant	M	E	E, I, AL, S
Canyon live oak	*Quercus chrysolepis* Liebm.	Tolerant	M	H	I, AL
Carolina silverbell	*Halesia carolina* L.	Tolerant	Perfect	E	U, E, I, M
Casuarina	*Casuarina* spp.	Intolerant	M, D	E	E, I, S
Cedar elm	*Ulmus crassifolia* Nutt.	Intermediate	Perfect	E	I, V
Cedro hembra	*Cedrela odorata* L.	Intolerant	Perfect	E	U

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[2] Flowering: M = Monoecious; D = Dioecious.

[3] Soil Orders: AL = Alfisols, AR = Andisols, E = Entisols, H = Histosols, I = Inceptisols, M = Mollisols, O = Oxisols, S = Spodosols, U = Ultisols, V = Vertisols.

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	**Scientific name**				
Cherrybark oak	*Quercus falcata* var. *pagodifolia* Ell.	Intolerant	M	H	AL, I
Chestnut oak	*Quercus prinus* L.	Intermediate	M	H	U, I
Chinkapin oak	*Quercus muehlenbergii* Engelm.	Intolerant	M	H	AL, I, M, U
Common persimmon	*Diospyros virginiana* L.	Very tolerant	D	E	AL, U, E, I
Corkbark fir	*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.	Tolerant	M	E	I, E, AL
Cucumbertree	*Magnolia acuminata* L.	Intermediate	Perfect	E	I, U
Digger pine	*Pinus sabiniana* Dougl.	Very intolerant	M	E	AL, E, I, M, U
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco	Intermediate	M	E	I, S, AL, M, E, U
Eastern cottonwood	*Populus deltoides* Bartr. ex Marsh. var. *deltoides*	Very intolerant	D	E	E, I
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	Very tolerant	M	E	S
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	Tolerant	M	E	S, AL, M, U, E, I
Eastern redbud	*Cercis canadensis* L.	Tolerant	Perfect	E	AL, M
Eastern redcedar	*Juniperus virginiana* L.	Intol.-Very Intol.	D	E	M, U
Eastern white pine	*Pinus strobus* L.	Intermediate	M	E	I, U, S, E, AL
Engelmann spruce	*Picea engelmannii* Parry ex Engelm.	Tolerant	M	E	I, E, AL, H
Eucalyptus grandis	*Eucalyptus grandis* Hile ex Maiden	Very Intolerant	Perfect	E	S
European alder	*Alnus glutinosa* (L.) Gaertn.	Intolerant	M	E	H, I, E
European black pine	*Pinus nigra* Arnold	Intolerant	M	E	AR, E, M, V
Florida maple	*Acer barbatum* Michx.	Tolerant	Polygamo-D	E	I, E, U
Florida torreya	*Torreya taxifolia* Arn.	Tolerant	D	H	AL, M
Flowering dogwood	*Cornus florida* L.	Very tolerant	Perfect	E	U, I, AL, S, E
Fraser fir	*Abies fraseri* (Pursh) Poir.	Very tolerant	M	E	I
Fraser magnolia	*Magnolia fraseri* Walt.	Intermediate	Perfect	E	I, U
Giant chinkapin	*Castanopsis chrysophylla* (Dougl.) A. DC.	Intermediate	M	H	I, E, U, AL
Giant sequoia	*Sequoiadendron giganteum* (Lindl.) Buchholz	Intolerant	M	E	I, AL
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.	Tolerant	M	E	S
Green ash	*Fraxinus pennsylvanica* Marsh.	Tolerant	D	E	I, E
Hackberry	*Celtis occidentalis* L.	Intermediate	Polygamo-M	E	M, E, I
Honeylocust	*Gleditsia triacanthos* L.	Intolerant	Polygamo-D	E	AL, I, M
Incense-cedar	*Libocedrus decurrens* Torr.	Intermediate	M	E	AL
Jack pine	*Pinus banksiana* Lamb.	Intolerant	M	E	S, E
Jeffrey pine	*Pinus jeffreyi* Grev. & Balf.	Intolerant	M	E	I, AL, E
Kiawe	*Prosopis pallida* (Humb. & Bonpl. ex Willd.) H.B.K.	Intolerant	Perfect	E	I, M, V
Koa	*Acacia koa* Gray	Intolerant	Perfect	E	I, H, U, O
Laurel	*Cordia alliodora* (Riuz & Pav.) Oken	Intolerant	Perfect	E	E, O, I, U, AL
Laurel oak	*Quercus laurifolia* Michx.	Tolerant	M	H	U, I
Limber pine	*Pinus flexilis* James	Intolerant	M	E	E
Live oak	*Quercus virginiana* Mill.	Intermediate	M	H	U, S, H, E
Loblolly-bay	*Gordonia lasianthus* (L.) Ellis	Tolerant	Perfect	E	S, I, U, H, E, M
Loblolly pine	*Pinus taeda* L.	Intolerant	M	E	U, E, S, AL
Lodgepole pine	*Pinus contorta* Dougl. ex Loud.	Very intolerant	M	E	I, AL, U, H
Longleaf pine	*Pinus palustris* Mill.	Intolerant	M	E	U, E, S
Maria	*Calophyllum calaba* L.	Intermediate	Polygamous	H	I, O, AL
Melaleuca	*Melaleuca quinquenervia* (Cav.) S.T. Blake	Intolerant	Perfect	E	E, S, H, I, U, O
Mockernut hickory	*Carya tomentosa* (Poir.) Nutt.	Intolerant	M	H	U, I, M, AL
Monkey-pod	*Pithecellobium saman* (Jacq.) Benth.	Intolerant	Perfect	E	O, I
Monterey pine	*Pinus radiata* D. Don	Intermediate	M	E	M, U, E, AL
Mountain hemlock	*Tsuga mertensiana* (Bong.) Carr.	Tolerant	M	E	S, E, I, H
Noble fir	*Abies procera* Rehd.	Intermediate	M	E	S, I
Northern red oak	*Quercus rubra* L.	Intermediate	M	H	S, AL, I, M, U, E
Northern white-cedar	*Thuja occidentalis* L.	Tolerant	M	E	H, I, E
Nutmeg hickory	*Carya myristiciformis* (Michx. f.) Nutt.	Intolerant	M	H	AL, I

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	**Scientific name**				
Nuttall oak	*Quercus nuttallii* Palmer	Intolerant	M	H	I, E
Ogeechee tupelo	*Nyssa ogeche* Bartr. ex Marsh.	Intolerant	Polygamo-D	E	I
Ohia lehua	*Metrosideros polymorpha* Gaud.	Intolerant	Perfect	E	H, I, M, S, O, U, AL
Ohio buckeye	*Aesculus glabra* Willd.	Tolerant	Polygamo-M	H	AL
Oregon ash	*Fraxinus latifolia* Benth.	Intermediate	D	E	AL, I, M, U
Oregon white oak	*Quercus garryana* Dougl. ex Hook.	Intolerant	M	H	AL, I, M, U
Osage-orange	*Maclura pomifera* (Raf.) Schneid.	Intolerant	D	E	AL, U, V, M
Overcup oak	*Quercus lyrata* Walt.	Intermediate	M	H	I, AL
Pacific madrone	*Arbutus menziesii* Pursh	Intermediate	Perfect	E	AL, U, I
Pacific silver fir	*Abies amabilis* Dougl. ex Forbes	Very tolerant	M	E	H, E, I, S
Pacific yew	*Taxus brevifolia* Nutt.	Very tolerant	D	E	U, AL, I
Paper birch	*Betula papyrifera* Marsh.	Intolerant	M	E	S, I
Pecan	*Carya illinoensis* (Wangenh.) K. Koch	Intolerant	M	H	E, I, AL
Pignut hickory	*Carya glabra* (Mill.) Sweet	Intermediate	M	H	U, AL, M
Pin cherry	*Prunus pensylvanica* L.	Very intolerant	Perfect	E	I, S, AL, H, E, M
Pin oak	*Quercus palustris* Muenchh.	Intolerant	M	H	E, AL
Pinyon	*Pinus edulis* Engelm.	Intolerant	M	E	AL, I
Pitch pine	*Pinus rigida* Mill.	Intolerant	M	E	S, AL, E, U
Plains cottonwood	*Populus deltoides* var. *occidentalis* Rydb.	Very intolerant	D	E	E, M, AL, I
Pondcypress	*Taxodium distichum* var. *nutans* (Ait.) Sweet	Intermediate	M	E	S, U
Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws.	Intolerant	M	E	E, I, M, AL, U
Pond pine	*Pinus serotina* Michx.	Intolerant	M	E	U
Poplar hybrids	*Populus* spp.	Very intolerant	D	E	E, I, M, S, U
Port-Orford-cedar	*Chamaecyparis lawsoniana* (A. Murr.) Parl.	Tolerant	M	E	S, U, I
Post oak	*Quercus stellata* Wangenh.	Intolerant	M	H	U, AL
Pumpkin ash	*Fraxinus profunda* (Bush) Bush	Intermediate	D	E	AL, E, S, U
Quaking aspen	*Populus tremuloides* Michx.	Very intolerant	D, Perfect	E	AL, S, I, H
Red alder	*Alnus rubra* Bong.	Intolerant	M	E	I, E, AL, U, H
Redbay	*Persea borbonia* (L.) Spreng.	Tolerant	Perfect	H	H
Red maple	*Acer rubrum* L.	Tolerant	Polygamo-D	E	E, I, U, AL, S, H
Red mulberry	*Morus rubra* L.	Tolerant	M, D	E	AL, I, S, U
Red pine	*Pinus resinosa* Ait.	Intolerant	M	E	E, S, AL, I
Red spruce	*Picea rubens* Sarg.	Toler.-Very Toler.	M	E	S, I, H
Redwood	*Sequoia sempervirens* (D. Don) Endl.	Very tolerant	M	E	I, U
River birch	*Betula nigra* L.	Intolerant	M	E	E
Roble blanco	*Tabebuia heterophylla* (DC.) Britton	Intolerant	Perfect	E	I
Robusta eucalyptus	*Eucalyptus robusta* Sm.	Intolerant	Perfect	E	O, U, H, I
Rock elm	*Ulmus thomasii* Sarg.	Intermediate	Perfect	E	M, AL, S
Rocky Mountain juniper	*Juniperus scopulorum* Sarg.	Very intolerant	D	E	M
Rosegum eucalyptus	*Eucalyptus grandis* Hill ex Maiden	Very intolerant	Perfect	E	S
Royal paulownia	*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.	Intolerant	Perfect	E	AL
Saligna eucalyptus	*Eucalyptus saligna* Sm.	Very intolerant	Perfect	E	H, I, O, U
Sand pine	*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.	Intermediate	M	E	E
Sassafras	*Sassafras albidum* (Nutt.) Nees	Intolerant	D	H	E, AL, U
Scarlet oak	*Quercus coccinea* Muenchh.	Very intolerant	M	H	AL, I, U
Scotch pine	*Pinus sylvestris* L.	Intolerant	M (mostly)	E	S, E, I, H, AL, M
September elm	*Ulmus serotina* Sarg.	Tolerant	Perfect	E	U, AL, I
Shagbark hickory	*Carya ovata* (Mill.) K. Koch	Intermediate	M	H	U, AL, M
Shellbark hickory	*Carya laciniosa* (Michx. f.) Loud.	Very tolerant	M	H	AL
Shortleaf pine	*Pinus echinata* Mill.	Intolerant	M	E	U
Shumard oak	*Quercus shumardii* Buckl.	Intolerant	M	H	AL, I, V
Silk-oak	*Grevillea robusta* A. Cunn.	Very intolerant	Perfect	E	H, I, U
Silver maple	*Acer saccharinum* L.	Tolerant	Polygamous	E, H	S, I, M, H
Singleleaf pinyon	*Pinus monophylla* Torr. & Frem.	Intolerant	M	E	M

Tree species		Shade tolerance class	Flowering characteristic[2]	Germination, epigeal or hypogeal	Most common soil orders[3]
Common name	Scientific name				
Sitka spruce	*Picea sitchensis* (Bong.) Carr.	Tolerant	M	E	E, S, I, H
Slash pine	*Pinus elliottii* Engelm.	Intolerant	M	E	S, U, E
Slippery elm	*Ulmus rubra* Muhl.	Tolerant	Perfect	E	M, AL
Sourwood	*Oxydendrum arboreum* (L.) DC.	Tolerant	Perfect	E	U, I, E
Southern magnolia	*Magnolia grandiflora* L.	Tolerant	Perfect	E	S, AL, V, U
Southern redcedar	*Juniperus silicicola* (Small) Bailey	Intol.-Very intol.	D	E	AL, E, I, S, U
Southern red oak	*Quercus falcata* Michx. var. *falcata*	Intermediate	M	H	U, AL
Spruce pine	*Pinus glabra* Walt.	Very tolerant	M	E	S, E
Striped maple	*Acer pensylvanicum* L.	Very tolerant	M, D	E	I, AL, S, M
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.	Tolerant	M	E	I, E, AL
Sugarberry	*Celtis laevigata* Willd.	Tolerant	Polygamo-M	E	I, E
Sugar maple	*Acer saccharum* Marsh.	Very tolerant	Polygamous	E	S, AL, M
Sugar pine	*Pinus lambertiana* Dougl.	Intermediate	M	E	U, AL
Swamp chestnut oak	*Quercus michauxii* Nutt.	Intolerant	M	H	AL, I
Swamp cottonwood	*Populus heterophylla* L.	Intolerant	D	E	AL, I, E
Swamp tupelo	*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.	Intolerant	Polygamo-D	E	U, I, E
Swamp white oak	*Quercus bicolor* Willd.	Intermediate	M	H	E, I
Sweetbay	*Magnolia virginiana* L.	Intermediate	Perfect	E	U, S, H
Sweet birch	*Betula lenta* L.	Intolerant	M	E	S, I, U
Sweetgum	*Liquidambar styraciflua* L.	Intolerant	M	E	AL
Sycamore	*Platanus occidentalis* L.	Intermediate	M	E	E, I, AL, V, H, M
Table Mountain pine	*Pinus pungens* Lamb.	Intolerant	M	E	I
Tabonuco	*Dacryodes excelsa* Vahl	Intermediate	D	E	U
Tamarack	*Larix laricina* (Du Roi) K. Koch	Very intolerant	M	E	H, I, E
Tanoak	*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.	Tolerant	M	H	I, AL
Turkey oak	*Quercus laevis* Walt.	Intolerant	M	H	E
Virginia pine	*Pinus virginiana* Mill.	Intolerant	M	E	S, I
Water hickory	*Carya aquatica* (Michx. f.) Nutt.	Intermediate	M	H	I
Water oak	*Quercus nigra* L.	Intolerant	M	H	I
Water tupelo	*Nyssa aquatica* L.	Intolerant	Polygamo-D	E	AL, E, H, I
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.	Very tolerant	M	E	AL, E, H, I, S, U
Western juniper	*Juniperus occidentalis* Hook.	Intolerant	M	E	M, AR, E, V
Western larch	*Larix occidentalis* Nutt.	Very intolerant	M	E	I, AL, S
Western redcedar	*Thuja plicata* Donn ex D. Don	Very tolerant	M	E	I, U, H
Western white pine	*Pinus monticola* Dougl. ex D. Don	Intermediate	M	E	S
White ash	*Fraxinus americana* L.	Intolerant	D	E	AL, S, I
White basswood	*Tilia heterophylla* Vent.	Tolerant	Perfect	E	I, U, AL, E, M
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	Tolerant	M	E	I, E, AL, U
White oak	*Quercus alba* L.	Intermediate	M	H	AL, U
White spruce	*Picea glauca* (Moench) Voss	Intermediate	M	E	AL, I
Whitebark pine	*Pinus albicaulis* Engelm.	Intermediate	M	E	I, E, M
Willow oak	*Quercus phellos* L.	Intolerant	M	H	I, AL
Winged elm	*Ulmus alata* Michx.	Tolerant	Perfect	E	AL, U
Yagrumo hembra	*Cecropia peltata* L.	Intolerant	D	E	U, M, AL, O, I
Yagrumo macho	*Didymopanax morototoni* (Aubl.) Dcne. & Planch.	Intolerant	Perfect	E	E, U, I, M
Yellow birch	*Betula alleghaniensis* Britton	Intermediate	M	E	S, I, AL
Yellow buckeye	*Aesculus octandra* Marsh.	Tolerant	Polygamo-M	H	AL, E
Yellow-poplar	*Liriodendron tulipifera* L.	Intolerant	Perfect	E	I, U

Checklist of Insects and Mites

Scientific name	Common name[1]
Abebaea cervella Walsingham	(a leafroller moth)
Abgrallaspis ithacae (Ferris)	hemlock scale
Acantholyda erythrocephala (Linnaeus)	pine false webworm
Acantholyda pini Rohwer	(a web-spinning sawfly)
Acantholyda zappei (Rohwer)	(nesting-pine sawfly)
Acleris chalybeana (Fernald)	(a leafroller moth)
Acleris gloverana (Walsingham)	western blackheaded budworm
Acrobasis betulella Hulst	birch tubemaker
Acrobasis caryivorella Ragonot	(a casebearer)
Acrobasis demotella Grote	walnut shoot moth
Acrobasis juglandis (LeBaron)	pecan leaf casebearer
Acronicta americana (Harris)	American dagger moth
Acronicta lepusculina Guenee	cottonwood dagger moth
Actias luna (Linnaeus)	luna moth
Adelges abietis (Linnaeus)	eastern spruce gall adelgid
Adelges cooleyi (Gillette)	Cooley spruce gall adelgid
Adelges nordmannianae (Eckstein)	(a gall)
Adelges nusslini (Borner)	(a woolly aphid)
Adelges piceae (Ratzeburg)	balsam woolly adelgid
Aethes rutilana (Hubner)	pale juniper webworm
Agrilus acutipennis Mannerheim	(a flatheaded borer)
Agrilus angelicus Horn	(Pacific oak twig girdler)
Agrilus anxius Gory	bronze birch borer
Agrilus arcuatus torquatus LeConte	(hickory spiral borer)
Agrilus bilineatus (Weber)	twolined chestnut borer
Agrilus burkei Fisher	(a flatheaded borer)
Agrilus cephalicus LeConte	(a flatheaded borer)
Agrilus difficilis Gory	(a flatheaded borer)
Agrilus fuscipennis Gory	(a flatheaded borer)
Agrilus horni Kerremans	(a flatheaded borer)
Agrilus liragus Barter & Brown	bronze poplar borer
Agrilus otiosus Say	(a flatheaded borer)
Agrilus politus (Say)	(a flatheaded borer)
Agromyza albitarsis Meigen	(a leafminer fly)
Aleuroplatus coronatus (Quaintance)	(crown whitefly)
Alniphagus aspericollis (LeConte)	alder bark beetle
Alsophila pometaria (Harris)	fall cankerworm
Altica ambiens LeConte	alder flea beetle
Amblycerus robiniae (Fabricius)	(a seed beetle)
Amphibolips confluenta (Harris)	large oak-apple wasp
Amphicerus bicaudatus (Say)	apple twig borer
Anacampsis niveopulvella (Chambers)	(a gelechiid moth)
Anacamptodes pergacilis (Hulst)	(a looper)
Andricus quercuscalifornicus (Bassett)	(a gall wasp)
Aneflormorpha subpubescens (LeConte)	(oak stem borer)
Anisococcus crawi (Coquillett)	(white sage mealybug)
Anisota rubicunda (Fabricius)	(green-striped mapleworm)
Anisota senatoria (J. E. Smith)	orangestriped oakworm
Anisota stigma (Fabricius)	spiny oakworm
Anisota virginiensis (Drury)	pinkstriped oakworm
Anomala oblivia Horn	pine chafer
Anoplonyx laricivorus (Rohwer & Middleton)	(twolined larch sawfly)
Anoplonyx occidens Ross	(western larch sawfly)
Anthaxia aeneogaster Laporte & Gory	(a flatheaded twig borer)
Antispila nysaefoliella Clemens	tupelo leafminer
Antron douglasii (Ashmead)	(spined turban gall)
Aphis gossypii Glover	cotton aphid, melon aphid
Aphis maculatae (Fitch)	(spotted poplar aphid)
Aphrophora parallela (Say)	pine spittlebug
Aphrophora saratogensis (Fitch)	Saratoga spittlebug
Apteromechus ferratus (Say)	(a wood-boring weevil)
Araecerus levipennis Jordan	koa haole seed weevil
Archips argyrospila (Walker)	fruittree leafroller
Archips fervidana (Clemens)	oak webworm
Archips negundana (Dyar)	(a leafroller)
Archodontes melanopus (Linnaeus)	(a roundheaded borer)
Argyresthia laricella Kearfott	(larch shoot moth)
Argyresthia thuiella (Packard)	arborvitae leafminer
Argyrotaenia juglandana (Fernald)	hickory leafroller
Argyrotaenia pinatubana (Kearfott)	pine tube moth
Argyrotaenia quercifoliana (Fitch)	(a leaf roller)
Argyrotaenia tabulana Freeman	(lodgepole needletier)
Arrhenodes minutus (Drury)	oak timberworm
Artipus floridanus Horn	(leaf notcher weevil)
Ascalapha odorata (Linnaeus)	black witch
Asphondylia ilicicola Foote	(a gall midge)
Asterocampa celtis (Boisduval & LeConte)	(hackberry butterfly)
Asterolecanium minus Lindinger	(a pit scale)
Asterolecanium pustulans (Cockerell)	oleander pit scale
Asterolecanium puteanum Russell	(holly pit scale)
Asterolecanium quercicola (Bouché)	(a pit scale)
Asterolecanium variolosum (Ratzeburg)	golden oak scale
Atimia confusa dorsalis LeConte	(a roundheaded borer)
Atimia confusa maritima Linsley	(a roundheaded borer)
Atimia huachucae Champlain and Knull	(a roundheaded borer)
Atimia vandykei Linsley	(a roundheaded borer)
Atta texana (Buckley)	Texas leafcutting ant
Atteva punctella (Cramer)	(ailanthus webworm)
Augomonoctenus libocedrii Rohwer	(incense-cedar cone sawfly)
Automeris io (Fabricius)	io moth
Azteca alfari Emery	(an ant)
Azteca constructor Emery	(an ant)
Baliosus ruber Weber	basswood leafminer
Barbara colfaxiana (Kearfott)	Douglas-fir cone moth

Scientific name	Common name[1]
Barbara mappana Freeman	(cone moth)
Bassettia ligni Kinsey	(a gall wasp)
Besbicus mirabilis (Kinsey)	(a gall wasp)
Bucculatrix albertiella Busck	(oak ribbedcase maker)
Bucculatrix canadensisella Chambers	birch skeletonizer
Bucculatrix recognita Braun	(an oak skeletonizer)
Buprestis aurulenta Linnaeus	golden buprestid
Caliroa lineata MacGillivary	(pin oak sawfly)
Caliroa quercuscoccineae Dyar	scarlet oak sawfly
Callidium hoppingi Linsley	(a roundheaded borer)
Callidium juniperi Fisher	(a roundheaded borer)
Callidium texanum Schaeffer	(a roundheaded borer)
Calligrapha scalaris (LeConte)	elm calligrapha
Callirhopalus bifasciatus (Roelofs)	(Japanese weevil)
Callirhytis cornigera (Osten Sacken)	(horned oak gall)
Callirhytis perdens (Kinsey)	(a gall wasp)
Callirhytis quercuspunctata (Bassett)	(gouty oak gall)
Caloptilia negundella (Chambers)	(boxelder leafroller)
Cameraria umbellulariae (Walsingham)	(a leafblotch miner)
Camponotus ferrugineus (Fabricius)	red carpenter ant
Camponotus pennsylvanicus (De Geer)	black carpenter ant
Canarsia ulmiarrosorella (Clem.)	(a pyralid moth)
Carulaspis juniperi (Bouche)	juniper scale
Carynota stupida (Walker)	(a treehopper)
Caryobruchus gleditsiae (Linnaeus)	(a seed beetle)
Caryomyia holotricha (Osten Sacken)	(a gall midge)
Caryomyia sanguinolenta (Osten Sacken)	(a gall midge)
Caryomyia tubicola (Osten Sacken)	(a gall midge)
Cecidomyia piniinopis Osten Sacken	(gouty pitch midge)
Cecidomyia reeksi Vockeroth	(a gall midge)
Ceratomia undulosa (Walker)	(a sphinx moth)
Ceresium unicolor (Fabricius)	(a roundheaded borer)
Chaitophorus populicola (Thomas)	(an aphid)
Chalcophorella campestris (Say)	(flatheaded sycamore-heartwood borer)
Chionaspis americana Johnson	elm scurfy scale
Chionaspis corni Cooley	dogwood scale
Chionaspis lintneri Comstock	(linter scale)
Chionaspis pinifoliae (Fitch)	pine needle scale
Choristoneura conflictana (Walker)	large aspen tortrix
Choristoneura fumiferana (Clemens)	spruce budworm
Choristoneura lambertiana (Busck)	(sugar pine tortrix)
Choristoneura occidentalis Freeman	western spruce budworm
Choristoneura pinus Freeman	jack pine budworm
Choristoneura retiniana (Walsingham)	(modoc budworm)
Choristoneura rosaceana (Harris)	obliquebanded leafroller
Chrysobothris azurea LeConte	(a flatheaded borer)
Chrysobothris femorata (Olivier)	flatheaded appletree borer
Chrysobothris mali Horn	Pacific flatheaded borer
Chrysobothris nixa Horn	(flatheaded cedar borer)
Chrysobothris sexsignata (Say)	(a flatheaded borer)
Chrysobothris texana LeConte	(a flatheaded borer)
Chrysobothris tranquebarica (Gmelin)	Australian pine borer
Chrysomela crotchi Brown	aspen leaf beetle
Chrysomela scripta Fabricius	cottonwood leaf beetle
Chrysomphalus obscurus	(obscure scale)
Chrysoteuchia topiaria (Zeller)	cranberry girdler
Cimbex americana Leach	elm sawfly
Cinara coloradensis (Gillette)	(black polished spruce aphid)
Cinara fornacula Hottes	green spruce aphid
Cinara sabinae (Gillette & Palmer)	(Rocky Mountain juniper aphid)
Cinara strobi (Fitch)	white pine aphid
Cinara tujafilina (del Guercio)	(an aphid)
Citheronia regalis (Fabricius)	regal moth
Clastoptera undulata Uhler	(a spittlebug)
Cnidocampa flavescens (Walker)	oriental moth
Coleophora laricella (Hubner)	larch casebearer
Coleophora serratella (Linnaeus)	(birch casebearer)
Coleophora ulmifoliella McDunnough	elm casebearer
Coleotechnites edulicola Hodges & Stevens	(pinyon needle miner)
Coleotechnites juniperella (Kearfott)	(a gelechiid moth)
Coleotechnites milleri (Busck)	lodgepole needleminer
Coleotechnites occidentis (Freeman)	(a gelechiid moth)
Coleotechnites piceaella (Kearfott)	(a gelechiid moth)
Coleotechnites thujaella (Kearfott)	(a gelechiid moth)
Colopha ulmicola (Fitch)	elm cockscomb gall aphid
Coloradia pandora Blake	pandora moth
Conophthorus banksianae McPherson	jack pine tip beetle
Conophthorus coniperda (Schwarz)	white pine cone beetle
Conophthorus edulis Hopkins	piñon cone beetle
Conophthorus lambertianae Hopkins	sugar pine cone beetle
Conophthorus monophyllae Hopkins	(single leaf piñon cone beetle)
Conophthorus monticolae Hopkins	mountain pine cone beetle
Conophthorus ponderosae Hopkins	ponderosa pine cone beetle
Conophthorus radiatae Hopkins	Monterey pine cone beetle
Conotrachelus affinis Boheman	(a hickory nut weevil)
Conotrachelus aratus (Germar)	(a snout weevil)
Conotrachelus hicoriae Schoof	(a snout weevil)

Scientific name	Common name[1]
Conotrachelus juglandis LeConte	butternut curculio
Conotrachelus naso LeConte	(a snout weevil)
Conotrachelus posticatus Boheman	(a snout weevil)
Conotrachelus retentus (Say)	black walnut curculio
Contarinia cerasiserotinae (Osten Sacken)	(a gall midge)
Contarinia juniperina Felt	juniper midge
Contarinia negundifolia Felt	(boxelder gall midge)
Contarinia oregonensis Foote	(Douglas-fir cone midge)
Contarinia washingtonensis Johnson	(cone scale midge)
Coptotermes niger Snyder	(a termite moth)
Correbidia terminalis Hampson	(a ctenuchid moth)
Corthylus columbianus Hopkins	Columbian timber beetle
Corythucha aesculi O. & D.	(a lace bug)
Corythucha arcuata (Say)	oak lace bug
Corythucha ciliata (Say)	sycamore lace bug
Corythucha juglandis (Fitch)	(a walnut lace bug)
Corythucha pallipes Parshley	(a birch lace bug)
Cossula magnifica (Strecker)	pecan carpenterworm
Croesia semipurpurana (Kearfott)	oak leaftier
Croesus latitarsus Norton	dusky birch sawfly
Cryptococcus fagisuga Lindinger	beech scale
Cryptophlebia illepida (Butler)	koa seedworm
Cryptorhynchus lapathi (Linnaeus)	poplar-and-willow borer
Cryptotermes brevis (Walker)	West Indian drywood termite
Cudonigera houstonana (Grote)	(a budworm moth)
Curculio caryae (Horn)	pecan weevil
Curculio longidens (Chittenden)	(a snout weevil)
Curculio pardalis Chittenden	(a snout weevil)
Curculio sulcatulus (Casey)	(a snout weevil)
Curculio uniformis (LeConte)	filbert weevil
Cylindrocopturus eatoni Buchanan	(pine reproduction weevil)
Cyrtepistomus castaneus (Roelofs)	Asiatic oak weevil
Dasineura balsamicola (Lintner)	(balsam gall midge)
Dasineura rachiphaga Tripp	(spruce cone axis midge)
Dasychira basiflava (Packard)	(dark tussock moth)
Datana integerrima Grote & Robinson	walnut caterpillar
Datana ministra (Drury)	yellownecked caterpillar
Dendrocoris pini Montandon	(a stink bug)
Dendroctonus adjunctus Blandford	roundheaded pine beetle
Dendroctonus approximatus Dietz	Mexican pine beetle
Dendroctonus brevicomis LeConte	western pine beetle
Dendroctonus frontalis Zimmermann	southern pine beetle
Dendroctonus jeffreyi Hopkins	Jeffrey pine beetle
Dendroctonus ponderosae Hopkins	mountain pine beetle
Dendroctonus pseudotsugae Hopkins	Douglas-fir beetle

Scientific name	Common name[1]
Dendroctonus rufipennis (Kirby)	spruce beetle
Dendroctonus simplex LeConte	eastern larch beetle
Dendroctonus terebrans (Olivier)	black turpentine beetle
Dendroctonus valens LeConte	red turpentine beetle
Derocrepis aesculi (Drury)	(a flea beetle)
Desmia funeralis (Hubner)	grape leaffolder
Diapheromera femorata (Say)	walkingstick
Diaphnocoris chlorionis (Say)	honeylocust plant bug
Dicerca divaricata (Say)	(a flatheaded borer)
Dicerca lurida (Fabricius)	(a flatheaded borer)
Dicerca tenebrica (Kirby)	(a flatheaded borer)
Dichelonyx valida LeConte	(a scarab beetle)
Dichomeris marginella (Fabricius)	juniper webworm
Dictyla montropidia (Stal)	(Spanish elm lacewing bug)
Dioryctria abietivorella (Grote)	(fir coneworm)
Dioryctria albovittella (Hulst)	(a coneworm)
Dioryctria amatella (Hulst)	southern pine coneworm
Dioryctria pygmaeella Ragonot	baldcypress coneworm
Dioryctria reniculelloides Mutuura & Munroe	spruce coneworm
Dioryctria resinosella Mutuura	red pine shoot moth
Dioryctria yatesi Mutuura & Munroe	(mountain pine coneworm)
Dioryctria zimmermani (Grote)	Zimmerman pine moth
Diplotaxis sordida (Say)	(a scarab beetle)
Diprion frutetorum Fabricius	(a sawfly)
Diprion similis (Hartig)	introduced pine sawfly
Dorcaschema alternatum (Say)	(a roundheaded borer)
Dorcaschema wildii Uhler	(mulberry borer)
Dryocoetes affaber (Mannerheim)	(a bark beetle)
Dryocoetes betulae Hopkins	birch bark beetle
Dryocoetes confusus Swaine	western balsam bark beetle
Dysmicoccus wistariae Green	(a mealybug)
Earomyia abietum McAlpine	(fir seed maggot)
Earomyia barbara McAlpine	(a cone maggot)
Earomyia longistylata McAlpine	(a cone maggot)
Ecdytolopha insiticiana Zeller	locust twig borer
Ectropis crepuscularia (D. & S.)	(saddleback looper)
Elaphidionoides villosus (Fabricius)	(twig pruner)
Elasmuche lateralis (Say)	(a stink bug)
Elatobium abietinum (Walker)	spruce aphid
Empoasca pergandei Gillette	(a leafhopper)
Enaphalodes rufulus (Haldeman)	red oak borer
Ennomos magnaria Guenee	(notched-wing geometer)
Ennomos subsignaria (Hubner)	elm spanworm
Eotetranychus multidigituli (Ewing)	(a spider mite)
Epimecis hortaria (Fabricius)	(a looper)
Epinotia aceriella (Clemens)	maple trumpet skeletonizer
Epinotia meritana Heinrich	white fir needleminer
Epinotia nanana (Treitschke)	(a skeletonizer)
Epinotia subviridis Heinrich	(cypress leaftier)
Erannis tiliaria (Harris)	linden looper
Eriocampa ovata (Linnaeus)	(alder woolly sawfly)
Eriosoma lanigerum (Hausmann)	woolly apple aphid
Eriosoma rileyi Thomas	(woolly elm bark aphid)
Essigella gillettei Hottes	(an aphid)
Euceraphis betulae Koch	(an aphid)

Scientific name	Common name[1]
Eucosma bobana Kearfott	(pinyon pine cone borer)
Eucosma gloriola Heinrich	eastern pine shoot borer
Eucosma rescissoriana (Heinrich)	(lodgepole pine cone borer)
Eucosma siskiyouana (Kearfott)	(fir cone borer)
Eucosma sonomana Kearfott	western pineshoot borer
Eucosma tocullionana Heinrich	white pine cone borer
Eupithecia spermaphaga (Dyar)	fir cone looper
Euproctis chrysorrhoea (Linnaeus)	browntail moth
Eurytetranychus admes Prichard & Baker	(a spider mite)
Euzophera magnolialis Capps	(a pyralid moth)
Euzophera ostricolorella Hulst	(a pyralid moth)
Euzophera semifuneralis (Walker)	American plum borer
Exoteleia pinifoliella (Chambers)	pine needleminer
Fagiphagus imbricator (Fitch)	beech blight aphid
Fascista cercerisella (Chambers)	redbud leaffolder
Fenusa dohrnii (Tischbein)	European alder leafminer
Fenusa pusilla (Lepeletier)	birch leafminer
Ferrisia virgata Cockerell	striped mealybug
Formica exsectoides Forel	Allegheny mound ant
Galenara consimilis (Heinrich)	(New Mexico fir looper)
Gibbobruchus mimus (Say)	(a seed beetle)
Gilpinia hercyniae (Hartig)	European spruce sawfly
Gloveria arizonensis Packard	(a tent caterpillar)
Glycobius speciosus (Say)	sugar maple borer
Glyptoscelis aridis Van Dyke	(a leaf beetle)
Glyptoscelis vandykei Krauss	(a leaf beetle)
Gnathotrichus retusus (LeConte)	(an ambrosia beetle)
Gnathotrichus sulcatus (LeConte)	(an ambrosia beetle)
Goes pulcher (Haldeman)	(living-hickory borer)
Goes pulverulentus (Haldeman)	(living-beech borer)
Goes tesselatus (Haldeman)	oak sapling borer
Goes tigrinus (DeGeer)	white oak borer
Gonioctena americana (Schaeffer)	American aspen beetle
Gossyparia spuria (Modeer)	European elm scale
Gynaecia dirce (Linnaeus)	(a nymphalid butterfly)
Gypsonoma haimbachiana (Kearfott)	cottonwood twig borer
Halisidota argentata subalpina French	(a tiger moth)
Halisidota harrisii Walsh	sycamore tussock moth
Halisidota ingens Hy. Edwards	(a tiger moth)
Hemiberlesia rapax (Comstock)	greedy scale
Hemichroa crocea (Geoffroy)	striped alder sawfly
Hemicoelus spp.	powderpost beetle
Henricus fuscodorsanus (Kearfott)	(cone cochylid)
Heterarthrus nemoratus (Fallen)	(birch leaf-mining sawfly)
Heterocampa guttivitta (Walker)	saddled prominent
Heterocampa manteo (Doubleday)	variable oakleaf caterpillar
Heterotermes convexinotatus Snyder	(a termite)
Heterotermes tennis Hagan	(a termite)

Scientific name	Common name[1]
Historis odius (Fabricius)	(a nymphalid butterfly)
Homadaula anisocentra Meyrick	mimosa webworm
Hyalophora cecropia (Linnaeus)	cecropia moth
Hydria prunivorata (Ferguson)	(cherry scallop shell moth)
Hylecoetus lugubris Say	sapwood timberworm
Hylemya (Lasiomma) antracina (Czerny)	(spruce cone maggot)
Hylesinus oregonus (Blackman)	(Oregon ash bark beetle)
Hylobius pales (Herbst)	pales weevil
Hylobius radicis Buchanan	pine root collar weevil
Hylobius rhizophagus M., B., & W.	pine root tip weevil
Hylobius warreni Wood	(Warren's collar weevil)
Hylurgopinus rufipes (Eichhoff)	native elm bark beetle
Hyperaspis signata (Olivier)	(a ladybird beetle)
Hyphantria cunea (Drury)	fall webworm
Icerya purchasi Maskell	cottony cushion scale
Ichthyura inclusa (Hubner)	poplar tentmaker
Illinoia liriodendri Monell	tuliptree aphid
Ips calligraphus (Germar)	(sixspined ips)
Ips confusus (LeConte)	(piñon ips)
Ips emarginatus (LeConte)	(emarginate ips)
Ips grandicollis (Eichhoff)	(southern pine engraver)
Ips latidens (LeConte)	(a bark beetle)
Ips lecontei Swaine	(Arizona fivespined ips)
Ips mexicanus (Hopkins)	(Monterey pine ips)
Ips montanus (Eichhoff)	(an engraver beetle)
Ips paraconfusus Lanier	California fivespined ips
Ips pilifrons Swaine	(an engraver beetle)
Ips pini (Say)	pine engraver
Ips plastographus (LeConte)	(California fourspined ips)
Ips spinifer (Eichhoff)	(an engraver beetle)
Itame pustularia (Guenee)	(a spanworm)
Janus abbreviatus (Say)	willow shoot sawfly
Kaltenbachiella ulmifusa (Walsh & Riley)	(a gall aphid)
Kermes pubescens Bogue	(a scale insect)
Kleidocerys resedae germinatus (Say)	(a lygaeid bug)
Knulliana cincta (Drury)	banded hickory borer
Lambdina athasaria pellucidaria (Grote & Robinson)	(a geometrid)
Lambdina fiscellaria fiscellaria (Guenee)	hemlock looper
Lambdina fiscellaria lugubrosa (Hulst)	western hemlock looper
Lambdina fiscellaria somniaria (Hulst)	western oak looper
Lambdina pellucidaria (Grote & Robinson)	(a geometrid)
Laspeyresia bracteatana (Fernald)	fir seed moth
Laspeyresia caryana (Fitch)	hickory shuckworm
Laspeyresia injectiva (Heinrich)	(Jeffrey pine seedworm)
Laspeyresia piperana (Kearfott)	(ponderosa pine seedworm)
Laspeyresia populana Busck	(a bark moth)
Laspeyresia youngana (Kearfott)	spruce seed moth
Lecanium fletcheri Ckll.	(a scale insect)
Leperisinus aculeatus (Say)	(eastern ash bark beetle)
Lepidosaphes ulmi (Linnaeus)	oystershell scale
Leptocoris trivittatus (Say)	boxelder bug

Scientific name	Common name[1]
Leptoglossus corculus (Say)	(southern pine seed bug)
Leptoypha minor McAtee	(Arizona ash lace bug)
Leucoma salicis (Linnaeus)	satin moth
Lithocolletis salicifoliella Chambers	(a leafblotch miner)
Lithophane antennata (Walker)	green fruitworm
Longistigma caryae (Harris)	giant bark aphid
Lymantria dispar (Linnaeus)	gypsy moth
Macrohaltica ambiens (LeConte)	alder flea beetle
Magdalis gentilis LeConte	(a weevil)
Magicicada septendecim (Linnaeus)	periodical cicada
Malacosoma americanum (Fabricius)	eastern tent caterpillar
Malacosoma californicum (Packard)	western tent caterpillar
Malacosoma constrictum (Hy. Edwards)	Pacific tent caterpillar
Malacosoma disstria Hubner	forest tent caterpillar
Maladera castanea (Arrow)	Asiatic garden beetle
Marmara arbutiella Busck	(a twig and leaf miner)
Matsucoccus acalyptus Herbert	(piñon pine scale)
Matsucoccos bisetosus Morrison	(two seta pine scale)
Matsucoccus californicus Morrison	(California pine scale)
Matsucoccus fasciculensis Herbert	(fascicle pine scale)
Matsucoccus gallicola Morrison	(pine twig gall scale)
Matsucoccus monophyllae McKenzie	(a scale)
Matsucoccus paucicicatrices Morrison	(sugar pine scale)
Matsucoccus resinosae Bean & Godwin	red pine scale
Mayetiola carpophaga (Tripp)	(spruce seed midge)
Mayetiola thujae (Hedlin)	(a gall midge)
Megacyllene caryae (Gahan)	painted hickory borer
Magacyllene robiniae (Forster)	locust borer
Megastigmus atedius Walker	(a seed chalcid)
Megastigmus laricis Marcovitch	(a seed chalcid)
Megastigmus lasiocarpae Crosby	(a seed chalcid)
Megastigmus pinus Parfitt	(fir seed chalcid)
Megastigmus specularis Walley	(balsam fir seed chalcid)
Megastigmus spermotrophus Wachtl	(Douglas-fir seed chalcid)
Megastigmus tsugae Crosby	(a seed chalcid)
Malalgus confertus (LeConte)	(a false powderpost beetle)
Melanaspis obscura (Comstock)	obscure scale
Melanaspis tenebricosa (Comstock)	gloomy scale
Melanolophia imitata (Walker)	(greenstriped forest looper)
Melanophila californica Van Dyke	California flatheaded borer
Melanophila drummondi (Kirby)	flatheaded fir borer
Melanophila fulvoguttata (Harris)	hemlock borer
Melipotis indomita (Walker)	(a caterpillar)
Melissopus latiferreanus (Walsingham)	filbertworm
Mesa populifoliella (Townsend)	(a leafmining sawfly)
Mesolecanium nigrofasciatum (Pergande)	terrapin scale

Scientific name	Common name[1]
Mimosestes amicus (Horn)	(a seed beetle)
Monocesta coryli (Say)	larger elm leaf beetle
Monochamus spp.	(a wood borer)
Monoctenus melliceps (Cresson)	(a sawfly)
Mordvilkoja vagabunda (Walsh)	poplar vagabond aphid
Mycetococcus ehrhorni (Cockerell)	(Ehrhorn's oak scale)
Myrmelachista ramulorum Wheeler	(an ant)
Nasutitermes corniger Motschulsky	(a termite)
Nematocampa limbata (Haworth)	filament bearer
Nematus currani Ross	(a sawfly)
Nematus ventralis Say	willow sawfly
Neoclytus acuminatus (Fabricius)	redheaded ash borer
Neoclytus caprea (Say)	(banded ash borer)
Neodiprion abbotii (Leach)	(a sawfly)
Neodiprion approximatus Hopkins	(northern pine weevil)
Neodiprion burkei Middleton	lodgepole sawfly
Neodiprion compar (Leach)	(a sawfly)
Neodiprion dubiosus Schedl	brownheaded jack pine sawfly
Neodiprion edulicolus Ross	(piñon sawfly)
Neodiprion excitans Rohwer	blackheaded pine sawfly
Neodiprion lecontei (Fitch)	redheaded pine sawfly
Neodiprion nanulus nanulus Schedl	red pine sawfly
Neodiprion nigroscutum Middleton	(a sawfly)
Neodiprion pinetum (Norton)	white pine sawfly
Neodiprion pinusrigidae (Norton)	(a sawfly)
Neodiprion pratti banksianae Rohwer	jack pine sawfly
Neodiprion pratti paradoxicus Ross	(a sawfly)
Neodiprion pratti pratti (Dyar)	Virginia pine sawfly
Neodiprion sertifer (Geoffroy)	European pine sawfly
Neodiprion swainei Middleton	Swaine jack pine sawfly
Neodiprion taedae linearis Ross	loblolly pine sawfly
Neodiprion tsugae Middleton	hemlock sawfly
Neolecanium cornuparvum (Thro)	magnolia scale
Neophasia menapia (Felder & Felder)	pine butterfly
Nepytia canosaria (Walker)	false hemlock looper
Nepytia phantasmaria (Strecker)	phantom hemlock looper
Nerice bidentata Walker	(a notodontid moth)
Neuroterus saltatorius (Hy. Edwards)	(a jumping gall wasp)
Neurotoma fasciata (Norton)	(a web-spinning sawfly)
Norape ovina (Sepp)	(a flannel moth)
Nuculaspis californica (Coleman)	black pineleaf scale
Nygmia phaeorrhoea (Donov)	brown-tail moth
Nymphalis antiopa (Linnaeus)	mourningcloak butterfly
Oberea ferruginea Casey	willow-branch borer
Oberea schaumi LeConte	(a roundheaded borer)
Oberea tripunctata (Swederus)	dogwood twig borer
Obrussa ochrefasciella (Chambers)	hard maple budminer

Scientific name	Common name[1]
Odontopus calceatus (Say)	(a snout beetle)
Odontota dorsalis (Thunberg)	locust leafminer
Oecanthus fultoni T. J. Walker	snowy tree cricket
Oeme rigida (Say)	(a roundheaded borer)
Olesicampe benefactor Hinz	(an ichneumonid parasite)
Oligonychus ilicis (McGregor)	southern red mite
Oligonychus ununguis (Jacobi)	spruce spider mite
Oligotrophus betheli Felt	juniper tip midge
Oncideres cingulata (Say)	twig girdler
Oncideres pustulata LeConte	(huisache girdler)
Operophtera bruceata (Hulst)	Bruce spanworm
Orgyia leucostigma (J. E. Smith)	whitemarked tussock moth
Orgyia pseudotsugata (McDunnough)	Douglas-fir tussock moth
Orgyia vetusta (Boisduval)	western tussock moth
Otiorhynchus ovatus (Linnaeus)	strawberry root weevil
Otiorhynchus sulcatus (Fabricius)	black vine weevil
Pachylobius picivorus (Germar)	pitch-eating weevil
Pachypsylla celtidisgemma Riley	budgall psyllid
Pachypsylla celtidismamma (Riley)	(hackberry nipplegall maker)
Pachypsylla celtidisvesicula Riley	(blistergall psyllid)
Pachypsylla venusta (Osten Sacken)	(petiolegall psyllid)
Paleacrita vernata (Peck)	spring cankerworm
Pandemis cerasana (Hubner)	(a leafroller moth)
Pantographa limata Grote & Robinson	basswood leafroller
Pantomorus cervinus (Boheman)	Fuller rose beetle
Paraclemensia acerifoliella (Fitch)	maple leafcutter
Paradiplosis tumifex Gagne	(balsam gall midge)
Paranthrene dollii dollii (Newman)	(a clearwing moth)
Paranthrene simulans (Grote)	(clearwing borer)
Paranthrene tabaniformis (Rottenberg)	(a clearwing moth)
Parorgyia plagiata Walker	pine tussock moth
Parthenolecanium corni (Bouche)	European fruit lecanium
Parthenolecanium fletcheri (Cockerell)	Fletcher scale
Pentamerismus erythreus (Ewing)	(a false spider mite)
Periphyllus lyropictus (Kessler)	Norway maple aphid
Periphyllus negundinis (Thomas)	boxelder aphid
Periploca atrata Hodges	(a moth)
Pero behrensaria (Packard)	(a spanworm)
Petrova albicapitana arizonensis (Heinrich)	(piñon pitch nodule moth)
Petrova sabiniana (Kearfott)	(a pitch nodule moth)
Phenacoccus acericola King	(maple phenacoccus)
Phigalia titea Cram.	half wing geometer
Phloeosinus canadensis Swaine	(a bark beetle)
Phloeosinus cristatus (LeConte)	(cypress bark beetle)
Phloeosinus cupressi Hopkins	(a bark beetle)
Phloeosinus dentatus (Say)	(eastern juniper bark beetle)
Phloeosinus hoferi Blackman	(a bark beetle)
Phloeosinus scopulorum Swaine	(a bark beetle)
Phloeosinus sequoiae Hopkins	(redwood bark beetle)
Phloeosinus serratus (LeConte)	(a bark beetle)
Phloeosinus taxodii Blackman	(southern cypress beetle)
Phloeotribus liminaris (Harris)	peach bark beetle
Phoracantha semipunctata (Fabricius)	(a wood borer)
Phryganidia californica Packard	California oakworm
Phyllobius intrusus Kono	arborvitae weevil
Phyllobius oblongus (Linnaeus)	(European snout beetle)
Phyllocnistis magnoliella Fabricius	(a leafminer)
Phyllocnistis populiella Chambers	(aspen leafminer)
Phyllocolpa bozemani (Cooley)	(poplar leaffolding sawfly)
Phyllonorycter tremuloidiella Braun	(aspen blotch miner)
Phyllophaga forsteri Burmeister	(a scarab beetle)
Phylloxera caryaecaulis (Fitch)	(hickory gall aphid)
Phymatodes aeneus LeConte	(a roundheaded borer)
Phymatodes nitidus LeConte	(a roundheaded borer)
Phytobia pruinosa (Coquillett)	(a leafminer fly)
Phytobia pruni (Grossenbacher)	(a leafminer fly)
Phytobia setosa (Loew)	(a cambium miner)
Phytomyza ilicicola Loew	native holly leafminer
Pikonema alaskensis (Rohwer)	yellowheaded spruce sawfly
Pikonema dimmockii (Cresson)	greenheaded spruce sawfly
Pineus coloradensis (Gillette)	(a woolly aphid)
Pineus patchae Borner	(a gall)
Pineus pinifoliae (Fitch)	pine leaf adelgid
Pissodes approximatus Hopkins	northern pine weevil
Pissodes dubius Randall	(a snout beetle)
Pissodes radiatae Hopkins	Monterey pine ips
Pissodes strobi (Peck)	white pine weevil
Pissodes terminalis Hopping	lodgepole terminal weevil
Pityogenes carinulatus LeConte	(a bark beetle)
Pityogenes fossifrons (LeConte)	(a bark beetle)
Pityophthorus lautus (Eichhoff)	(a bark beetle)
Pityophthorus liquidambarus Blackman	(a bark beetle)
Pityophthorus nitidus Swaine	(a bark beetle)
Pityophthorus toralis (Wood)	(a bark beetle)
Placosternus crinicornis (Chevrolat)	kiawe roundheaded borer
Plagiodera versicolora (Laicharting)	imported willow leaf beetle
Plagithmysus bilineatus Sharp	(a roundheaded borer)
Plagodis serinaria Herrich-Schaeffer	(a spanworm)
Platypus compositus (Say)	(a pinhole borer)
Platypus quadridentatus (Olivier)	(a pinhole borer)
Plectrodera scalator (Fabricius)	cottonwood borer
Pleuroptya salicalis (Guenee)	(a pyralid moth)
Podosesia syringae (Harris)	ash borer, lilac borer
Poecilonota cyanipes (Say)	(a flatheaded borer)
Poecilonota montana Chamberlin	(a flatheaded borer)
Polycanon stoutii (LeConte)	(a false powderpost beetle)
Polydesma umbricola Boisduval	monkeypod moth
Polygraphus rufipennis (Kirby)	(foureyed spruce beetle)
Popillia japonica Newman	Japanese beetle

Scientific name	Common name[1]
Prionoxystus macmurtrei (Guerin)	little carpenterworm
Prionoxystus robiniae (Peck)	carpenterworm
Prionus imbricornis (Linnaeus)	tilehorned prionus
Prionus laticollis (Drury)	broadnecked root borer
Pristiphora erichsonii (Hartig)	larch sawfly
Pristocauthophilus pacificus Thomas	mushroom camel cricket
Probole amicaria (Herrich-Schaeffer)	(a geometrid moth)
Prociphilus americanus (Walker)	(an aphid)
Prociphilus tesselatus (Fitch)	(woolly alder aphid)
Prodiplosis morrisi Gagne	(a poplar gall midge)
Profenusa lucifex (Ross)	(a leaf miner)
Profenusa thomsoni (Konow)	(a birch leaf mining sawfly)
Prosapia bicincta (Say)	twolined spittlebug
Protalebra tabebuiae Dozier	(a leafhopper)
Proteoteras willingana Kearfott	(boxelder twig borer)
Pseudococcus comstocki (Kuwana)	comstock mealybug
Pseudococcus maritimus Ehrhorn	grape mealybug
Pseudohylesinus dispar Blackman	(a bark beetle)
Pseudohylesinus granulatus (LeConte)	(fir root bark beetle)
Pseudohylesinus nobilis Swaine	(noble fir bark beetle)
Pseudohylesinus sericeus (Mannerheim)	(silver fir beetle)
Psylla uncatoides Ferris & Klyver	acacia psyllid
Ptilinus basalis LeConte	(a powderpost beetle)
Ptosima gibbicollis (Say)	(a flatheaded borer)
Pulvinaria acericola (Walsh & Riley)	(cottony maple leaf scale)
Pulvinaria innumerabilis (Rathvon)	cottony maple scale
Puto cupressi (Coleman)	(fir mealybug)
Puto pricei McKenzie	(price mealybug)
Pyrrhalta cavicollis (LeConte)	cherry leaf beetle
Pyrrhalta decora (Say)	(a leaf beetle)
Pyrrhalta decora decora (Say)	gray willow leaf beetle
Pyrrhalta luteola (Muller)	elm leaf beetle
Pyrrhalta punctipennis (Mannerheim)	(a leaf beetle)
Quadraspidiotus juglansregiae (Comstock)	walnut scale
Quadraspidiotus perniciosus (Comstock)	San Jose scale
Quernaspis quercus (Comstock)	(oak scale)
Resseliella clavula Beutenmuller	(a gall midge)
Rhabdophaga swainei Felt	spruce bud midge
Rheumaptera hastata (Linnaeus)	spearmarked black moth
Rhyacionia adana Heinrich	(a pine shoot moth)
Rhyacionia buoliana (Schiffermuller)	European pine shoot moth
Rhyacionia frustrana (Comstock)	Nantucket pine tip moth
Rhyacionia rigidana (Fernald)	pitch pine tip moth
Rhyacionia zozana Kearfott	(ponderosa pine tip moth)
Sabulodes aegrotata (Guenee)	omnivorous looper
Samia cynthia (Drury)	cynthia moth
Sannina uroceriformis Walker	persimmon borer

Scientific name	Common name[1]
Saperda calcarata Say	poplar borer
Saperda discoidea Fabricius	(a roundheaded borer)
Saperda inornata Say	(poplar gall borer)
Saperda moesta LeConte	(a roundheaded borer)
Saperda tridentata Olivier	elm borer
Saperda vestita Say	linden borer
Scaphoideus luteolus Van Duzee	whitebanded elm leafhopper
Schizura concinna (J. E. Smith)	redhumped caterpillar
Sciaphila duplex (Walsingham)	(aspen leaftier)
Sciaphilus asperatus (Bonsdorff)	(a weevil)
Scobicia bidentata (Horn)	(a false powderpost beetle)
Scolytus laricis Blackman	(larch engraver)
Scolytus mali (Bechstein)	larger shothole borer
Scolytus multistriatus (Marsham)	smaller European elm bark beetle
Scolytus muticus Say	hackberry engraver
Scolytus quadrispinosus Say	hickory bark beetle
Scolytus ventralis LeConte	fir engraver
Scotorythra paludicola (Butler)	koa moth
Seinarctica echo (J. E. Smith)	(a webworm)
Semanotus amethystinus (LeConte)	(amethyst cedar borer)
Semanotus juniperi (Fisher)	(a roundheaded borer)
Semanotus ligneus (Fabricius)	cedartree borer
Semiothisa sexmaculata incolorata (Dyar)	(larch looper)
Semudobia betulae (Winnertz)	(a birch midge)
Smodicum cucujiforme (Say)	(flat powderpost beetle)
Sparganothis acerivorana MacKay	(a leafroller)
Sparganothis dilutocostana (Walsingham)	(a leafroller)
Sparganothis reticulatana (Clemens)	(a leafroller moth)
Sphinx chersis (Hubner)	great ash sphinx
Sphinx kalmiae J. E. Smith	(a sphinx moth)
Sphinx sequoiae Boisduval	(a sphinx moth)
Stator limbatus (Horn)	(a seed beetle)
Stenodontes dasytomus (Say)	(hardwood stump borer)
Steremnius carinatus (Boheman)	(a weevil)
Stictocephala militaris Gibson & Wells	(a treehopper)
Stilpnotia salicis Linnaeus	satin moth
Styloxus bicolor (Champlain & Knull)	(juniper twig pruner)
Symmerista albifrons (J. E. Smith)	(an oakworm)
Symmerista canicosta Franclemont (=*albicosta* Hbn.)	(redhumped oakworm)
Synanthedon acerni (Clemens)	maple callus borer
Synanthedon pictipes (Grote & Robinson)	lesser peachtree borer
Synanthedon scitula (Harris)	dogwood borer
Synanthedon sequoiae (Hy. Edwards)	(sequoia pitch moth)
Synaphaeta guexi (LeConte)	(a roundheaded borer)
Syntexis libocedrii Rohwer	incense-cedar wasp
Systena marginalis (Illiger)	(a leaf beetle)

Scientific name	Common name[1]
Taniva abolineana (Kearfott)	(spruce needle miner)
Tegolophus spongiosus Styer	(a mite)
Tethida barda (Say)	blackheaded ash sawfly
Tetralopha asperatella (Clemens)	(a webworm)
Tetralopha robustella Zeller	pine webworm
Tetraneura ulmi (Linnaeus)	(a gall aphid)
Tetranychus canadensis (McGregor)	fourspotted spider mite
Tetranychus magnoliae Boud.	spider mite
Tetranychus urticae Koch	twospotted spider mite
Tetropium abietis Fall	roundheaded fir borer
Tetropium velutinum LeConte	(western larch borer)
Tetyra bipunctata (Herrich-Schaeffer)	shieldbacked pine seedbug
Thrips madronii Moulton	(a narrowwinged thrips)
Thyridopteryx ephemeraeformis (Haworth)	bagworm
Thysanoes fimbricornis LeConte	(a bark beetle)
Tinocallis ulmifolii (Monell)	elm leaf aphid
Tomostethus multicinctus (Rohwer)	brownheaded ash sawfly
Toumeyella liriodendri (Gmelin)	tuliptree scale
Toumeyella parvicornis (Cockerell)	pine tortoise scale
Trachykele blondeli Marseul	(western cedar borer)
Trachykele opulenta Fall	(a flatheaded borer)
Trioza magnoliae (Ashmead)	(a psyllid)
Trisetacus floridanus Keifer	(a mite)
Trisetacus neoquadrisetus Smith	(a mite)
Trisetacus quadrisetus (Thomas)	(juniper berry mite)
Tropidosteptes pacificus (Van Duzee)	(a plant bug)
Trypodendron betulae Swaine	(an ambrosia beetle)
Trypodendron lineatum (Olivier)	striped ambrosia beetle
Trypodendron retusum (LeConte)	(an ambrosia beetle)
Tuberculatus columbiae Richards	(an aphid)
Tylonotus bimaculatus Haldeman	(ash and privet borer)
Vaga blackburni (Tuely)	Blackburn butterfly
Valentinia glandulella (Riley)	(acorn moth)
Vasates aceris-crummena Riley	(a bladdergall mite)
Vasates quadripedes Shimer	maple bladdergall mite
Vespamima sequoiae (Hy. Edwards)	(sequoia pitch moth)
Walshomyia insignis Felt	(a gall midge)
Walshomyia sabinae (Patterson)	(a gall midge)
Xestobium spp.	powderpost beetle
Xiphydria abdominalis Say	(a horntail)
Xiphydria maculata Say	(a horntail)
Xyleborinus saxesensi (Ratzeburg)	(an ambrosia beetle)
Xyleborus affinis Eichhoff	(an ambrosia beetle)
Xyleborus ferrugineus (Fabricius)	(an ambrosia beetle)
Xyleborus simillimus Perkins	(an ambrosia beetle)
Xylobiops basilaris (Say)	(a false powderpost beetle)
Xylococculus betulae (Pergande)	(birch margarodid)
Xylosandrus compactus (Eichhoff)	black twig borer
Xylosandrus germanus (Blandford)	(an ambrosia beetle)
Xyloterinus politus (Say)	(an ambrosia beetle)
Xylotrechus aceris Fisher	gallmaking maple borer
Xylotrechus obliteratus LeConte	(poplar-butt borer)
Xystrocera globosa (Olivier)	monkeypod roundheaded borer
Zadiprion rohweri (Middleton)	(a sawfly)
Zeiraphera improbana (Walker)	(larch bud moth)
Zelleria haimbachi Busck	pine needle sheathminer
Zeugophora scutellaris Suffrian	(a leaf beetle)
Zeuzera pyrina (Linnaeus)	leopard moth

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[1] Names without parentheses are approved by the Entomological Society of America.

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Checklist of Organisms Causing Tree Diseases

Scientific binomial	Synonym	Common name or symptom
Acremonium diospyri (Crand.) W. Gams	*Cephalosporium diospyri* Crand.	persimmon wilt
Actinopelte dryina (Sacc.) Hoehn.		Actinopelte leaf spot
Aecidium aesculi Ell. et Kellelm.		leaf spot
Agrobacterium tumefaciens (E. F. Smith et Town.) Conn.		crown gall
Alternaria tenuis Nees		Alternaria leaf and stem blight
Alerodiscus amorphus (Pers.: Fr.) Rab.		canker
Amphichaeta grevilleae Loos		silk-oak leaf spot
Anthostoma oreodaphnes		foliage discoloration
Apiosporium piniphilum Fckl.		sooty mold
Apiosporina morbosa (Schw.) von Arx	*Dibotryon morbosum* Th. et Syd.	black knot
Arceuthobium abietinum Engelm. ex Munz		fir dwarf mistletoe
Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. et Wiens		red fir dwarf mistletoe
Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. et Wiens		white fir dwarf mistletoe
Arceuthobium americanum Nutt. ex Engelm.		lodgepole pine dwarf mistletoe
Arceuthobium californicum Hawksw. et Wiens		sugar pine dwarf mistletoe
Arceuthobium campylopodium Engelm.		western dwarf mistletoe
Arceuthobium cyanocarpum Coulter et Nelson		limber pine dwarf mistletoe
Arceuthobium divaricatum Engelm.		pinyon dwarf mistletoe
Arceuthobium douglasii Engelm.		Douglas-fir dwarf mistletoe
Arceuthobium laricis (Piper) St. Johns		larch dwarf mistletoe
Arceuthobium microcarpum (Engelm.) Hawkins et Wiens		western spruce dwarf mistletoe
Arceuthobium occidentale Engelm.		digger pine dwarf mistletoe
Arceuthobium pusillum Pk.		eastern dwarf mistletoe
Arceuthobium tsugense (Rosend.) G. N. Jones		hemlock dwarf mistletoe
Arceuthobium vaginatum (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. et Wiens		southwestern dwarf mistletoe
Arceuthobium vaginatum (Willd.) Presl subsp. *vaginatum*		southwestern dwarf mistletoe
Armillaria mellea (Vahl.: Fr.) Kumm.	*Armillariella mellea* (Vahl.: Fr.) Karst.	shoestring root rot
Armillaria ostoyae (Romagn.) Herink		root disease
Ascochyta cornicola Sacc.		Ascochyta leaf blight
Astraeus pteridis (Shear) Zeller		earth star
Atropellis pinicola Zell. et Good.		Atropellis canker
Atropellis piniphila (Weir) Lohm. et Cash		branch canker
Atropellis tingens Lohm. et Cash		stem canker
Aureobasidium pullulans (de B.) Arn.	*Pullularia pullulans* (de B.) Berkh.	hemlock seed mold
Bifusella linearis (Pk.) Hoehn.		needle cast
Bifusella saccata (Darker) Darker		needle cast
Boletellus zelleri (Murr.) Sing.		mycorrhizal symbiont
Botryodiplodia theobromae Pat.		Botryodiplodia canker
Botryosphaeria dothidea (Moug.: Fr.) Ces. et deNot		madrone canker
Botryosphaeria ribis (Tode: Fr.) Gross. et Dug.		canker & trunk lesion
Botrytis cinerea Pers.: Fr.		Botrytis petal blight
Calonectria crotalariae (Loos) Bell et Sobers		koa crown rot
Calonectria thea Loos		koa shoot blight
Capnodium pini Berk. et Curt.		sooty mold
Cenangium furruginosum Fr.		Cenangium limb canker
Cenococcum graniforme (Sow.) Ferd. et Winge		mycorrhizal symbiont
Cephalosporium pallidum Verrall		wood stain fungus
Ceratocystis ambrosia Bak.		Ceratocystis canker
Ceratocystis cana (Muench) C. Mor.		Ceratocystis canker

Scientific binomial	Synonym	Common name or symptom
Ceratocystis coerulescens (Muench) Bak.		sapstreak
Ceratocystis crassivaginata H. D. Griffin		Ceratocystis canker
Ceratocystis fagacearum (Bretz) Hunt		oak wilt
Ceratocystis fimbriata Ell. et Halst.		Ceratocystis canker
Ceratocystis moniliformis (Hedg.) C. Mor.		Ceratocystis canker
Ceratocystis piceae (Muench) Bak.		Ceratocystis canker
Ceratocystis pluriannulata (Hedg.) C. Mor.		sapwood stain
Ceratocystis serpens (Goid.) C. Mor.		Ceratocystis canker
Ceratocystis tremul-aurea Davidson et Hinds		Ceratocystis canker
Ceratocystis ulmi (Buism.) C. Mor.		Dutch elm disease
Cercospora aesculina Ell. et Kellerm.		leaf spot
Cercospora circumcissa Sacc.		leaf spot
Cercospora cornicola Tr. et Earle		dogwood leaf spot
Cercospora halstedii Ell. et Ev.		leaf blotch
Cercospora maclurae Ell. et Ev.		leaf spot
Cercospora microsora Sacc.		basswood leaf spot
Cercospora pulvinula Cke. et Ell.		holly leaf spot
Cercospora sequoiae Ell. et Ev.		foliage blight
Cercospora spegazzinii Sacc.		leaf spot
Cercosporella celtidis (Ell. et Kellerm.) J. J. Davis		leaf spot
Cerotelium fici (Butl.) Arth.		leaf spot
Ceuthocarpum conflictum (Cke.) Berl.		leaf spot
Chlorogenus robiniae Holmes		witches' broom virus
Chrysomyxa arctostaphyli Diet.		yellow witches' broom
Chrysomyxa chiogenis Arth.		needle rust
Chrysomyxa empetri Pers.		needle rust
Chrysomyxa ilicina (Arth.) Arth.		holly rust
Chrysomyxa ledi de B.		needle rust
Chrysomyxa ledicola Lagh.		spruce needle rust
Chrysomyxa pirolata Wint.		spruce cone rust
Chrysomyxa weirii Jacks.		needle rust
Chrysomyxa woroninii Tranz.		bud rust
Ciboria acerina Whetz. et Buchew.		maple flower blight
Cladosporium effusum (Wint.) Dem.		pecan scab
Cladosporium humile J. J. Davis		leaf spot
Climacocystis borealis (Fr.) Kotl. et Pouz.	*Polyporus borealis* Fr.	heart rot
Climacodon septentrionalis (Fr.) Karst.	*Hydnum septentrionalis* Fr.	white heart rot
Clitocybe tabescens (Scop.: Fr.) Bres.	*Armillaria tabescens* (Scop.: Fr.) Bres.	mushroom root rot
Coccomyces hiemalis Higg.		cherry leaf spot
Coccomyces lutescens Higg.		cherry leaf spot
Coleosporium asterum (Diet.) Syd.	*Coleosporium solidaginis* (Schw.) Thum.	needle rust
Coleosporium campanulae (Pers.) Lev.		needle rust
Coleosporium crowellii Cumm.		needle rust
Coleosporium helianthi (Schw.) Arth.		needle rust
Coleosporium jonesii (Pk.) Arth.		needle rust
Coleosporium madiae Cke.		tarweed rust
Colletotrichum gloeosporioides Penz.		leaf spot
Collybia velutipes (Fr.) Kumm.	*Flammulina velutipes* (Fr.) Karst.	heart rot
Coniophora corrugis Burt		sapwood and heartwood rot
Coniophora olivacea (Fr.) Karst.	*Coniophorella olivacea* (Fr.) Karst.	root and butt rot
Coniophora puteana (Schum.: Fr.) Karst	*Coniophorella puteana* Schum.: Fr.	root and butt rot
Conophilis americana (L.) Wallr.	*Coniophora cerebella* (Pers.) Pers.	root rot squaw root
Conothyrium truncisedum Vestergr.		leaf spot
Coprinus atramentarius (Bull: Fr.) Fr.		root rot
Corticium expallense Bres.	*Phlebia expallense* (Bres.) Parm.	decay fungus
Corticium salmonicolor Berk. et Br.	*Phanerochaete salmonicolor* (Berk. et Br.) Jülich	dieback

Scientific binomial	Synonym	Common name or symptom
Corynebacterium ilicis Mandel, Guba et Litsky		leaf and twig blight
Coryneum carpophyllum (Lev.) Jauch.		leaf spot
Criconemoides quadricornis (Kirhanova) Raski		ring nematode
Cristulariella depraedens (Cke.) Hoehn.		leaf spot
Cristulariella pyramidalis Wat. et Marsh.		target leaf spot
Cronartium coleosporioides (Diet. et Holw.) Arth.		pine stem rust
Cronartium comandrae Pk.		Comandra blister rust
Cronartium comptoniae Arth.		sweetfern rust
Cronartium occidentale Hedgc., Bethel et Hunt		pinyon blister rust
Cronartium quercuum (Berk.) Miy. ex Shirai f. sp. *fusiforme* Burds. et Snow	*Cronartium fusiforme* Hedgc. et Hunt	fusiform rust
Cronartium quercuum (Berk.) Miy. ex Shirai	*Cronartium quercuum* (Berk.) Miy. ex Shirai f. sp. *quercuum*	eastern gall rust
Cronartium ribicola Fischer		white pine blister rust
Cryphonectria cubensis (Bruner) Hodges	*Diaporthe cubensis* Bruner	eucalyptus canker
Cryphonectria parasitica (Murr.) Barr	*Endothia parasitica* (Murr.) P. J. et H. W. And.	chestnut blight
Cryptosphaeria populina (Pers.: Fr.) Sacc.		Cryptosphaeria canker
Cryptosporium pinicola Lind.		stem and branch canker
Cryptostroma corticale (Ell. et Ev.) Greg. et Wall.		sooty bark
Cucurbitaria staphula Dearn. ex Arnold et Russell		rough, corky bark
Cylindrocarpon cylindroides Wollenw.		stem and branch canker
Cylindrocladium floridanum Sob. et Seymour		Cylindrocladium root rot
Cylindrocladium scoparium Morg.		Cylindrocladium root rot
Cylindrosporium californicum Earle		leaf spot
Cylindrosporium defoliatum Heald et Wolf		leaf spot
Cylindrosporium juglandis Wolf		leaf spot
Cylindrosporium fraxini (Ell. et Kellerm.) Ell. et Ev.		leaf spot
Cytophoma pruinosa (Fr.) Hoehn.		ash canker
Cytospora abietis Sacc.		stem and branch canker
Cytospora ambiens Sacc.		twig fungus
Cytospora chrysosperma Pers.: Fr.		Cytospora canker
Cytospora leucostoma Sacc.		canker
Cytospora tumulosa Ell. et Ev.		branch saprophyte
Cytosporina ludibunda Sacc.		elm wilt and dieback
Daedalea ambigua Berk.	*Daedalea elegans* Spring.: Fr.	heart rot
Daedalea juniperina Murr.	*Antrodia juniperina* (Man.) Niem et Ryv.	heart rot
Daedalea quercina L.: Fr.		heart rot
Daedalea unicolor (Bull.: Fr.) Murr.	*Cerrena unicolor* (Bull.: Fr.) Murr.	canker rot
Dasyscypha agassizii (Berk. et Curt.) Sacc.		saprophyte on bark
Dasyscypha arida (Philli.) Sacc.		saprophyte on bark
Dasyscypha pini Hahn et Ayers		saprophyte on bark
Dasyscypha willkommii (Hart.) Rehm		European larch canker
Davisomycella ampla (Dav.) Darke		needle cast
Diaporthe alleghaniensis R. H. Arnold		black sunken canker and shoot blight
Dichomitus squalens (Karst.) Reid	*Polyporus anceps* Pk.	western root rot
Didymascella tetramicrospora Pant. et Darker		leaf blight
Didymascella thujina (Durand) Maine		seedling and foliage blight
Didymosphaeria oregonensis Good.		alder stem and branch canker
Dimerium juniperi Dearn.		smudge mold
Dimerosporium tsugae Dearn.		sooty mold of hemlock
Diplodia longispora Cke. et Ell.		twig blight

Scientific binomial	Synonym	Common name or symptom
Diplodia pinea (Desm.) Kickx	*Sphaeropsis sapinea* (Fr.: Fr.) Dyko et Sutton	Diplodia tip blight
Diplodia taxi (Sowerby) deNot.		stem canker
Diplodia tumefaciens (Shear) Zalasky		rough, corky bark
Discula quercina (Westd.) v. Arx		anthracnose
Dothichiza populea Sacc. et Briard.		Dothichiza canker
Dothiorella quercina (Cke. et Ell.) Sacc.		Dothiorella canker
Dothiorella ulmi Verr. et May		elm dieback
Dothistroma pini Hulb.		Dothistroma needle blight
Echinodontium taxodii (Lentz et McKay) Gross	*Stereum taxodii* Lentz et McKay	pecky cypress pocket rot
Echinodontium tinctorium (Ell. et Ev.) Ell. et Ev.		Indian paint fungus
Elaphomyces granulatus Fr.		mycorrhizal symbiont
Elsinoe corni Jenk. et Bitan.		dogwood leaf spot
Elsinoe quercus-falcatae J. Mill.		spot anthracnose
Elsinoe randii Jenk. et Bitan.		pecan spot anthracnose
Elytroderma deformans (Weir) Darker		needle cast
Encoeliopsis laricina (Ettl.) Groves		larch shoot blight
Endocronartium harknessii (J. P. Moore) Y. Hirat	*Peridermium harknessii* J. P. Moore	western gall rust
Endoraceium acaciae C.S. Hodges et D. E. Gardner		rust fungus
Endoraceium hawaiiense C.S. Hodges et D. E. Gardner		rust fungus
Endothia gyrosa (Schw.: Fr.) Fr.		pin oak blight
Endothia havaensis Bruner	*Cryphonectria havanensis* (Bruner) Barr	canker disease
Epifagus virginiana (L.) Bart.		beech drops
Erwinia nimipressuralis Cart.		elm wetwood
Erysiphe cichoracearum DC.		powdery mildew
Eutypella parasitica Davidson et Lorenz		Eutypella canker
Fabrella tsugae (Farl.) Kirschst.	*Didymascella tsugae* (Farl.) Maire	hemlock needle blight
Fomes fomentarius (L.: Fr.) Kickx		trunk rot
Fomes geotropus Cke.		heart rot
Fomes nobilissimus (Cke.) Lowe		trunk rot
Fomes sclerodermeus (Lev.) Cke.	*Fomes marmoratus* (Berk. et Curt.) Cke.	white heart rot
Fomes subroseus Weir	*Fomitopsis cajanden* (Karst.) Kotl. et Pous.; *Fomes cajanderi* Karst.	heart rot
Fomitopsis cajanden (Karst.) Kotl. et Pouz.	*Fomes subroseus* Weir; *Fomes cajanderi* Karst.	heart rot
Fomitopsis fraxineus (Bull.: Fr.)	*Fomes fraxineus* (Bull.: Fr.) Cke.	wood rot
Fomitopsis officinalis (Vill.: Fr.) Bond. et Singer	*Fomes officinalis* (Vill.: Fr.) Faull	quinine fungus
Fomitopsis pinicola (Schwartz: Fr.) Karst.	*Fomes pinicola* (Schwartz: Fr.) Cke.	red belt fungus
Fomitopsis roseus (Alb. et Schw.: Fr.) Karst.	*Fomes roseus* (Alb. et Schw.: Fr.) Karst.	heart rot
Fomitopsis scutellata (Schw.) Bond. et Sing.	*Fomes scutellatus* (Schw.) Cke.	wood rot
Fumago vagans Fr.		black mold
Fusarium oxysporum (Schl.) emend. Snyd. et Hans.		pecan feeder root necrosis
Fusarium reticulatum Mont. var. *negundinis* (Sherb.) Wr.	*Fusarium roseum* (Lk.) emend. Snyd. et Hans.	red stain of boxelder
Fusarium solani (Mart.) App. et Wr. emend. Snyd. et Hans.		pecan feeder root necrosis
Fusicoccum aesculi Corda in Sturm		madrone canker
Ganoderma applanatum (Pers.: Wallr.) Pat.	*Fomes applanatus* (Pers.: Wallr.) Gill	artist's conk
Ganoderma curtisii (Berk.) Murr.	*Polyporus curtisii* Berk.	root rot
Ganoderma lucidum (Leys. ex Fr.) Karst.		varnish or lacquer conk
Ganoderma tsugae Murr.	*Polyporus tsugae* (Murr.) Overh.	red varnish-top fungus
Gloeocystidiellum citrinum (Pers.) Donk	*Corticium radiosum* (Fr.: Pers.) Fr.	root and butt rot
Gloeocystidiellum radiosum		root and butt rot
Gloeosporium apocryptum Ell. et Ev.		anthracnose
Gloeosporium aridum Ell. et Holway		ash anthracnose

Scientific binomial	Synonym	Common name or symptom
Gloeosporium betularum Ell. et Mart.		anthracnose leaf blight
Gloeosporium saccharinum Ell. et Ev.		anthracnose
Gloeosporium ulmicolum Miles		leaf spot and twig blight
Glomus fasciculatus (Thaxter) Gerd. et Trappe		endomycorrhizal associate
Glomus mosseae (Nicol. et Gerd.) Gerd. et Trappe		endomycorrhizal associate
Gnomonia caryae Wolf		anthracnose
Gnomonia caryae var. *pecanae* Cole		pecan liver spot
Gnomonia leptostyla (Fr.) Ces. et deNot.		walnut anthracnose
Gnomonia nerviseda Cole		pecan vein spot
Gnomonia quercina Kleb.		oak anthracnose
Gnomonia satacea (Pers.: Fr.) Ces. et deNot.		canker, shoot blight, leaf spot
Gnomonia tiliae Kleb.		basswood anthracnose
Gnomonia ulmea (Schw.: Fr.) Thuem.		black spot of elm
Gnomonia veneta (Sacc. et Speg.) Kleb.	*Gnomonia paltani* Edg.	oak anthracnose
Gomphidius ochraceus Kauffm.		mycorrhizal symbiont
Gomphidius rutilus (Schael.: Fr.) Lund. & Nannf.		mycorrhizal symbiont
Gomphidius superiorensis Kauf. et Smith		mycorrhizal symbiont
Gomphidius vinicolor Pk.		mycorrhizal symbiont
Gremmeniella abietina (Lagerb.) Morelet	*Scleroderris lagerbergii* Grem.	Scleroderris canker
Guignardia aesculi (Pk.) Stew.		leaf blotch
Gymnopilus spectabilis (Fr.) Singer	*Pholiota spectabilis* (Fr.) Kumm.	trunk rot
Gymnosporangium bethelii Kern		juniper twig knot rust
Gymnosporangium biseptatum Ell.		stem and branch gall rust
Gymnosporangium clavipes (Cke. et Pk.) Cke. et Pk.		gall rust
Gymnosporangium effusum Kern		gall rust
Gymnosporangium ellisii (Berk.) Farlow		witches' broom rust
Gymnosporangium globosum Farlow		juniper branch gall rust
Gymnosporangium inconspicuum Kern		juniper witches' broom rust
Gymnosporangium juniperi-virginianae Schw.		cedar applerust
Gymnosporangium kernianum Bethel		brown rust
Gymnosporangium libocedri (P. Henn.) Kern		witches' broom rust
Gymnosporangium nelsonii Arth.		juniper stem gall rust
Gymnosporangium nidus-avis Thaxt.		juniper witches' broom rust
Haematostereum sanguinolentum (Alb. et Schw.: Fr.) Pouz.	*Stereum sanguinolentum* (Alb. et Schw.: Fr.) Fr.	red heart trunk rot
Helicobasidium purpureum (Tul.) Pat.		violet root rot
Hendersonula toruloidea Natt.		branch wilt and canker
Hericium coralloides (Scop.: Fr.) S. F. Gray	*Hydnum coralloides* Scop.: Fr.	trunk rot
Hericium erinaceum (Bull.: Fr.) Pers.	*Hydnum erinaceus* Bull.: Fr.	magnolia leaf spot
Herpotrichia nigra Hartig	*Herpotrichia juniperi* (Duby) Petrak	brown felt mold
Heterobasidion annosum (Fr.) Bref.	*Fomes annosus* (Fr.) Cke.	annosus root rot
Hirschioporus abietinus (Dicks.: Fr.) Donk	*Polyporus abietinus* Dicks.: Fr.	wood rot
Hydnum erinaceus Bull.: Fr.	*Hericium erinaceum* (Bull.: Fr.) Pers.	hedgehog fungus
Hymenochaete agglutinans Ell.		gluing fungus
Hypoderma hedgcokii Dearn.	*Ploioderma hedgcokii* (Dearn.) Darker	needle cast
Hypoderma lethale Dearn.	*Ploioderma lethale* (Dearn.) Darker	needle cast
Hypodermella laricis Tub.		larch needlecast
Hypoxylon mammatum (Wahl.) J. Miller	*Hypoxylon pruinatum* (Klot.) Cke.; *H. blakei* Berk. et Curt.	Hypoxylon canker
Hysterographium fraxini (Pers.: Fr.) deNot.		twig saprophyte
Inonotus andersonii (Ell. et Overh.) Cérny	*Poria andersonii* (Ell. et Ev.) Cérny	white pocket rot
Inonotus dryadeus (Pers.: Fr.) Murr.	*Polyporus dryadeus* Pers.: Fr.	white root rot
Inonotus dryophilus (Berk.) Murr.	*Polyporus dryophilus* Berk.	white pocket rot
Inonotus glomeratus (Pk.) Murr.	*Polyporus glomeratus* Pk.	wood rot

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Inonotus obliquus (Pers.: Fr.) Pilat	*Poria obliqua* (Pers.: Fr.) Karst.	heart rot
Inonotus rheades	*(Peniophora polygonia, americanum, rufa)*	trunk rot
Inonotus tomentosus (Fr.) Gilbertson	*Polyporus tomentosus* Fr.	heart rot
Kabatiella phoradendri Darker f. sp. *umbellulariae* Harv.		leaf spot
Keithia chamaecyparissi Adams	*Didymascella chamaecyparissi* (Adams) Maire	tip blight
Lachnellula occidentalis (Hahn et Ayers) Dharne		stem canker
Lachnellula suecica (de Bary ex Fuckel) Nannf.		stem canker
Laetiporus sulphureus (Bull.: Fr.) Bond et Singer	*Polyporus sulphureus* Bull.: Fr.	sulphur fungus
Lecanosticta acicola Theum. et Syd.		brown spot
Lentinus tigrinus Fr.		heart rot
Leuocytospora kunzei (Sacc.) Z. Urba	*(Cytospora kunzei* Sacc.)	branch canker
Linospora gleditsiae J. Miller et Wolf		tarry leaf spot
Lirula abietis-concoloris (Mayr ex Dearn.) Darker		needle cast
Lirula macrospora (Hartig) Darker	*Lophodermium filiforme* Darker	needle cast
Lirula punctata (Darker) Darker		needle cast
Lophodermella arcuata (Darker) Darker		needle cast
Lophodermella concolor (Darker) Darker		needle cast
Lophodermium autumnale Darker		needle cast
Lophodermium juniperinum (Fr.) deNot.		foliage necrosis
Lophodermium laricinum Duby		needle cast
Lophodermium nitens Darker		needle cast
Lophodermium piceae (Fckl.) Hoehn.		needle cast
Lophodermium pinastri (Schrad.) Chev.		needle cast
Lophodermium seditiosum Minter, Staley, et Millar		needle cast
Lophodermium uncinatum Darker		needle cast
Lophophacidium hyperboreum Lagerb.		snow blight
Macrophoma taxi Berl. et Vogl.		yellow needle blight
Macrophomina phaseoli (Maub.) Ashby		charcoal root rot
Marssonina brunnea (Ell. et Ev.) Sacc.		Marssonina leaf spot
Marssonina fraxini Niessl		leaf spot
Marssonina populi (Lib.) Magn.		leaf spot, shoot blight
Melampsora abietis-canadensis (Farlow) Ludw.		hemlock needle rust
Melampsora farlowii (Arth.) Davis		hemlock cone and shoot rust
Melampsora medusae Theum.		Melampsora leaf rust
Melampsorella caryophyllacearum Schroet.		fir broom rust
Melanconis juglandis (Ell. et Ev.) Graves		twig and branch dieback
Meliola koae Stevens		koa sooty mold
Meloidogyne incognita (Kof. et White) Chitw.		root knot
Meloidogyne ovalis Riffle		ash root knot nematode
Microsphaera alni DC.		powdery mildew
Microstroma juglandis (Berang.) Sacc.		white mold
Morsus ulmi Holmes		elm phloem necrosis
Mycosphaerella caryigena Dem. et Cole		downy spot
Mycosphaerella cercidicola (Ell. et Kellerm.) Wolf		redbud anthracnose
Mycosphaerella dendroides (Cke.) Dem. et Cole		leaf blotch
Mycosphaerella effigurata (Schw.) House		ash leaf spot
Mycosphaerella fraxinicola (Schw.) House		ash leaf spot
Mycosphaerella glauca (Cke.) Woronichin		leaf spot and twig blight
Mycosphaerella juglandis Kessler		leaf spot
Mycosphaerella maculiformis (Pers.: Fr.) Schroet.		leaf spot

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Mycosphaerella milleri Hodges et Haasis	*Cercospora magnoliae* Ell. et Hark. (Imperfect state)	angular leaf spot
Mycosphaerella mori Wolf		leaf spot
Mycosphaerella nyssaecola (Cke.) Wolf		leaf spot
Mycosphaerella sassafras (Ell. et Ev.) Bub. et Kab.		sassafras leaf spot
Mycosphaerella taxi (Cooke) Lind		needle blight
Myxosporium nitidum Berk. et Curt.		twig blight
Naemacyclus minor Butin		needle cast
Nectria cinnabarina Tode: Fr.		branch dieback
Nectria coccinea Pers.: Fr. var. *faginata* Lohm., Wats. et Ay.		beech canker
Nectria galligena Bres.		Nectria canker
Nectria magnoliae Lohm. et Hept.		magnolia canker
Nectria peziza (Tode: Fr.) Fr.	*Nectria umbellulariae* (Plowr.) Harkn.	stem canker, dieback needle cast
Neofabraea populi G. E. Thompson		canker
Neopeckia coulteri (Pk.) Sacc.		pine brown-felt snow mold
Ovularia maclurae Ell. et Langl.		Osage-orange leaf spot
Oxyporus populinus (Sokum.: Fr.) Donk	*Fomes connatus* (Weinm.: Fr.) Gill.	heart rot
Paxillus involutus (Batch: Fr.) Fr.		brown root rot
Pellicularia koleroga Cke.	*Corticium stevensii* Burt.	thread blight
Peniophora polygonia (Fr.) Bourd. et Galz.	*Crytochaete polygonia* (Pers.) Karst.	trunk rot
Peniophora pseudo-pini Weres. et Gibs.		red heartwood stain
Peniophora rufa (Fr.) Boidin		trunk rot
Peniophora septentrionalis Laur.		trunk rot
Perenniporia compacta (Overh.) Ryv. et Gilbn.		white pocket rot
Perenniporia fraxinea (Bull.: Fr.) Ryv.	*Fomes fraxineus* (Bull.: Fr.) Cke.	wood rot
Perenniporia fraxinophilus (Peck) Ryv.	*Fomes fraxinophilus* (Pk.) Cke.	ash heart rot
Peridermium cerebroides Meinecke		coastal gall rust
Peridermium filamentosum Pk.		limb rust
Peridermium harknessii J. P. Moore	*Endocronartium harknessii* (J. P. Moore) Y. Hirat.	western gall rust
Peridermium ornamentale Arth.	*Pucciniastrum goeppertianum* (Kuehn) Kleb.	
Peridermium rugosum H. Jackson		needle rust
Peridermium stalactiforme Arth. et Kern		stalactiform rust
Pezicula acericola (Pk.) Sacc.		leaf spot
Pezicula subcarnea Groves		leaf spot or twig blight
Phacidium curtissii (Berk. et Rav.) Luttr.		leaf spot
Phacidium infestans Karst.		snow blight
Phaeocryptopus gaeumanni (Rohde) Petr.		needle cast
Phaeocryptopus nudis Petr.		needle cast
Phaeolus schweinitzii (Fr.) Pat.	*Polyporus schweinitzii* Fr.	red brown butt rot
Phellinus everhartii (Ell. et Gall) A. Ames	*Fomes everhartii* (Ell. et Gall.) Schr. & Spauld.	heart rot
Phellinus ferruginosus (Schrad.: Fr.) Pat.	*Poria ferruginosa* (Schrad.: Fr.) Karst.	white rot of slash
Phellinus igniarius (L.: Fr.) Quel.	*Fomes igniarius* (L.: Fr.) Kickx	false tender fungus
Phellinus johnsonianus (Murr.) Ryv.	*Fomes densus* Lloyd	heart rot
Phellinus laevigatus (Fr.) Bourd. et Galz.	*Fomes igniarius laevigatus* (Fr.) Overh.	heart rot
Phellinus nigrolimitatus (Rom.) Bourd. et Galz.	*Fomes nigrolimitatus* (Rom.) Egel.	root and butt rot
Phellinus pini (Thore: Fr.) A. Ames	*Fomes pini* (Thore: Fr.) Karst.	red ring rot
Phellinus pomaceus (Pers.) Maire	*Fomes pomaceus* (Pers.) Lloyd	trunk rot
Phellinus prunicola (Murr.) Gilbn.	*Poria prunicola* (Murr.) Sacc. et Trott.	trunk rot
Phellinus punctatus (Fr.) Pilat	*Poria punctata* (Fr.) Karst.	white rot of slash
Phellinus ribis (Schum.: Fr.) Quel.	*Fomes ribis* (Schum.: Fr.) Gill.	white heart rot

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Phellinus rimosus (Berk.) Pilat	*Fomes rimosus* (Berk.) Cke.	heart rot
Phellinus robustus (Karst.) Bourd. et Galz.	*Fomes robustus* Karst.	heart rot
Phellinus texanus (Murr.) A. Ames	*Fomes texanus* (Murr.) Hedgc. et Long	heart rot
Phellinus tremulae (Bond.) Bond. et Boriss	*Fomes igniarius* (L.: Fr.) Kickx var. *populinus* (Neum.) Campb.	false tinder fungus
Phellinus weiri (Murr.) Gilbn.	*Poria weirii* (Murr.) Murr.	laminated root rot
Phibalis pruinosa (Ell. et Ev.) Kohn et Korf		sooty-bark canker
Phleospora celtidis Ell. & Morg.		leaf spot
Phlyctaena tiliae Dearn.		leaf spot
Pholiota alnicola (Fr.) Singer	*Flammula alnicola* (Fr.) Kumm.	root and butt rot
Pholiota aurivella (Batsch: Fr.) Kumm		
Pholiota destruens (Brond.) Gillet		heart rot
Pholiota hepatica (Huds.: Fr.) Singer	*Flammula alnicola* (Huds.: Fr.) Kumm.	beefsteak fungus
Pholiota limonella (Pk.) Sacc.	*Pholiota squarroso-adiposa* Lange	heart rot
Pholiota squarrosa (Muller: Fr.) Kumm.		root and butt rot
Phoma aposphaerioides Briard et Hariot		Phoma canker
Phoma harknessii Sacc.		bark saprophyte
Phoma hystrella Sacc.		yellow needle blight
Phoma pedunculi Ell. et Ev.		leaf spot
Phomopsis juniperovora Hahn		foliage blight
Phomopsis macrospora Kobayi & Chiba		Phomopsis canker
Phomopsis occulta Trav.		tip blight
Phoradendron bolleanum (Seem.) Eich. subsp. *densum* (Torr.) Fosb.		mistletoe
Phoradendron bolleanum (Seem.) Eich. subsp. *pauciflorum* (Torr.) Wiens		white fir mistletoe
Phoradendron flavescens (Pursh) Nutt.		eastern mistletoe
Phoradendron juniperinum Engelm. subsp. *juniperinum* Wiens		mistletoe
Phoradendron juniperinum Engelm. subsp. *libocedri* Wiens		incense-cedar mistletoe
Phoradendron longispicum Trel.		mistletoe
Phoradendron serotinum (Raf.) M. C. Johnst.		eastern leafy mistletoe
Phoradendron tomentosum (DC.) Gray		mistletoe
Phoradendron villosum (Nutt.) Nutt. subsp. *villosum* Wiens		western hairy mistletoe
Phyllachora perseae Hodges		redbay leaf spot
Phyllactinia corylea Pers.		powdery mildew
Phyllactinia guttata (Fr.) Lev.		powdery mildew
Phyllosticta celtidis Ell. et Kell.		leaf spot
Phyllosticta innumera Cke. et Harkn.		leaf spot
Phyllosticta maclurae Ell. et Ev.		leaf spot
Phyllosticta magnoliae Sacc.		magnolia leaf spot
Phyllosticta minima (Berk. et Curt.) Ell. et Ev.		tar spot
Phyllosticta opaca Ell. et Ev.		leaf spot
Phymatotrichum paulowniae Sacc.		leaf spot
Phymatotrichum omnivorum (Shear) Dugg.		Texas root rot
Physalospora gregaria Sacc.		twig blight
Physalospora ilicis (Schleich.: Fr.) Sacc.		leaf spot
Phytophthora cactorum (Leb. et Cohn) Schr.		damping-off
Phytophthora cinnamomi Rands		root rot
Phytophthora citricola Sevada		root rot
Phytophthora inflata Caros. et Tucker		elm canker
Phytophthora lateralis Tucker. et J. A. Milb.		root rot
Piggotia fraxini Berk. et Curt.		leaf spot
Piptoporus betulinus (Bull.: Fr.) Karst.	*Polyporus betulinus* Bull.: Fr.	heart rot
Pleurotus ostreatus (Jacq.: Fr.) Kumm.		oyster mushroom

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Pleurotus ulmarius (Bull.: Fr.) Kumm.		elm wood rot
Ploioderma hedgcokii (Dearn.) Darker	*Hypoderma hedgcokii* Dearn.	needle cast
Podosphaera oxyacanthae DC. var. *tridactyla* Wallr.		cherry powdery mildew
Pollaccia saliciperda (Allesch. et Tub.) v. Arx		willow blight
Polyporus abietinus Dicks.: Fr.	*Trichaptum abietinus* (Dicks.: Fr.) Ryv.	trunk rot
Polyporus adustus Willd.: Fr.	*Bjerkandera adusta* (Willd.: Fr.) Karst.	sapwood decay
Polyporus berkeleyi Fr.	*Bondarzewia berkeleyi* (Fr.) Bond et Singer	root rot
Polyporus caesius Schrad.: Fr.	*Postia caesia* (Schrad.: Fr.) Karst.	heart rot
Polyporus calkinsii (Murr.) Sacc. et Trott.		heart rot
Polyporus guttulatus Pk.		root rot
Polyporus hispidus Bull.: Fr.	*Inonotus hispidus* (Bull. ex Fr.) Karst.	hispidus canker
Polyporus lucidus Leys.: Fr.	*Ganoderma lucidum* (Leys. ex Fr.) Karst.	varnish or lacquer conk
Polyporus obtusus Berk.	*Spongipellis unicolor* (Schw.) Murr.	heart rot
Polyporus robiniophilus (Murr.) Lloyd	*Perenniporia robiniophila* (Murr.) Ryv.	heart rot
Polyporus squamosus Mich.: Fr.		scaly or saddleback fungus
Polyporus versicolor L.: Fr.	*Coriolus versicolor* (L.: Fr.) Quel.	sapwood decay
Poria albipellucida Baxt.	*Poria rivulosa* (Berk. et Curt.) Cke.	redwood ring rot
Poria asiatica (Pil.) Overh.		trunk rot
Poria ferruginosa (Schrad.: Fr.) Karst.	*Phellinus ferruginosus* (Schrad.: Fr.) Pat.	
Poria incrassata (Berk. et Curt.) Burt	*Serpula incrassata* (Berk. et Curt.) Donk	heart rot
Poria mutans (Pk.) Pk.		
Poria prunicola (Murr.) Sacc. et Trott.	*Phellinus prunicola* (Murr.) Gilbn.	trunk rot
Poria punctata (Fr.) Karst.	*Phellinus punctatus* (Fr.) Pilat	
Poria rimosa Murr.	*Diptomitoporus rimosus* (Murr.) Gilbn. et Ryv.	heart rot
Poria sequoiae Bonar		redwood trunk rot
Poria spiculosa Campb. et Davids.		canker rot of hickory and pecan
Poria subacida (Pk.) Sacc.	*Perenniporia subacida* (Pk.) Donk	white root conk
Pratylenchus penetrans Cobb		root lesion nematode
Pseudomonas lauracearum Harv.		leaf spot
Pseudomonas mori (Boy. et Lamb.) Stev.		bacterial leaf spot
Puccinia andropogonis Schw.		leaf rust
Puccinia cordiae Arth.		canker producing rust
Puccinia peridermiospora (Ell. et Tr.) Arth.		ash rust
Pucciniastrum epilobii Otth		needle rust
Pucciniastrum goeppertianum (Keuhn) Kleb.	*Peridermium ornamentale* Arth.	needle rust
Pucciniastrum hydrangeae (Berk. et Curt.) Arth.		hemlock needle rust
Pucciniastrum vaccinii (Wint.) Jorst.		hemlock needle rust
Pyrofomes demidoffii (Lev.) Kotl. et Pouz.	*Fomes juniperinus* (Schrenk) Sacc. et Syd.	heart rot
Pythium debaryanum Hesse		damping-off
Pythium irregulare Buism.		damping-off and root rot
Pythium ultimum Trow		damping-off
Pythium vexans de B.		root rot
Radulodon americanum Ryv.	*Radulodon caesearium* (Morg.) Ryvarden	trunk rot
Resinicium bicolor (Alb. & Schw.: Fr.) Parm.	*Odontia bicolor* (Alb. & Schw.) Bres.	white stringy rot
Retinocyclus abietis (Crouan) Graves et Wells		endophytic fungus
Rhabdocline pseudotsugae Syd.		needle cast
Rhizina undulata Fr.		root rot
Rhizoctonia crocorum (Pers.) DC. Fr.		root rot
Rhizoctonia solani Kuehn		damping-off
Rhizosphaera kalkoffii Bud.		needle cast
Rhytidiella baranyayi Funk et Zalasky		rough, corky bark
Rhytidiella moriformis Zalasky		rough bark
Rhytisma acerinum Pers.: Fr.		tar spot
Rhytisma punctatum Pers.: Fr.		tar spot
Rosellinia herpotrichioides Hept. et Davidson		grey mold
Russula delica Fr.		mycorrhizal symbiont
Russula xerampelina (Schaef.) Fr.		mycorrhizal symbiont

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Sarcotrichila alpina (Fuckel) Hoehn.		needle blight
Schizophyllum commune Fr.		sapwood rot
Schizoxylon microsporum Davidson et Lor.		Schizoxylon canker
Scirrhia acicola (Dearn.) Sigg.		brown spot
Scirrhia pini Funk et A. K. Parker		red band needle blight
Scleroderma hypogaeum Zeller		false puffball
Sclerotinia gracilipes (Cke.) Sacc.		sweetbay petal rot
Scytinostroma galactinum (Fr.) Donk	*Corticium galactinum* (Fr.) Burt	root and butt rot
Septobasidium burtii Lloyd		scale brown felt
Septobasidium pseudopedicellatum Burt		scale brown felt
Septogloeum celtidis Dearn.		leaf spot
Septoria aceris (Lib.) Berk. et Br.		leaf blister
Septoria angustissima Pk.		leaf spot
Septoria cornicola Desm.		dogwood leaf spot
Septoria musiva Pk.		septoria leaf spot
Septoria populicola Pk.		leaf spot and canker
Septoria quercicola (Desm.) Sacc.		oak leaf fungus
Septotinia podophyllina Wat.		leaf blotch
Serpula himantioides (Fr.) Karst.	*Merulius himantioides* Fr.	root and butt rot
Sirococcus clavigignenti-juglandacearum Nair, Kostichka, et Kuntz		butternut canker
Sirococcus strobilinus (Dearn.) Petr.		Sirococcus tip blight
Sphaerella umbellulariae Cke. et Harkn.		foliage discoloration
Sphaeropsis ulmicola Ell. et Ev.		elm canker
Sphaerotheca lanestris Harkn.		oak powdery mildew
Sphaerotheca phytophila Kellerm. et Swing.		powdery mildew
Sphaerulina taxi (Cke.) Mass.		yellow leaf scorch
Spongipellis delectans (Pk.) Murr.	*Polyporus delectans* Pk.	white rot of hardwoods
Spongipellis pachyodon (Pers.) Kotl. et Pouz.	*Irpex mollis* Berk. et Curt.	Irpex canker
Sporodesmium maclurae Thuem.		Osage orange leaf spot
Steccherinum septentrionale (Fr.) Banker	*Hydnum septentrionale* Fr	trunk rot
Stereum chailletii Pers.: Fr.	*Amylostereum chailletii* (Pers.: Fr.) Boid.	trunk rot
Stereum gausapatum (Fr.) Fr.		white heart rot
Stereum hirsutum (Willd.: Fr.) S. F. Gray		sapwood decay
Stereum murraii (Berk. et Curt.) Burt	*Cystostereum murraii* (Berk. et Curt.) Pouz.	trunk rot
Stereum sulcatum Burt	*Echinodontium sulcatum* (Burt) Gross	trunk rot
Strumella coryneoidea Sacc. et Wint.		Strumella canker
Suillus cothurnatus Sing.		mycorrhizal symbiont
Suillus granulatus (L.: Fr.) Kuntze	*Boletus granulatus* L.: Fr.	mycorrhizal symbiont
Suillus pictus (Pk.) Smith & Thiers	*Boletinus pictus* (Pk.) Smith & Thiers	mycorrhizal symbiont
Suillus subaureus (Pk.) Snell ex Slipp et Snell	*Boletus subaureus* (Pk.) Snell ex Slipp et Snell	mycorrhizal symbiont
Suillus subluteus (Pk.) Snell ex Slipp et Snell	*Boletus subluteus* Pk.	mycorrhizal symbiont
Taphrina caerulescens (Mont. et Desm.) Tul.		oak leaf blister
Taphrina carveri Jenk.		tar spot
Taphrina cerasi (Fckl.) Sadeb.		cherry leaf curl
Taphrina johansonii Sadeb.		catkin deformity
Taphrina populi-salicis Mix		yellow leaf blister
Thyronectria austro-americana (Speg.) Seeler		honeylocust wilt
Trametes serialis Fr.	*Coriolellus serialis* (Fr.) Murr.	heart rot
Tranzschelia pruni-spinosae (Pers.) Diet.		cherry rust
Tricholoma flavovirens (Pers.: Fr.) Lund.		mycorrhizal symbiont
Tuber griseum Pers.: Fr.	*Tuber magnatum* Pico in Vitt.	mycorrhizal symbiont
Tuber melanosporum Vitt.		mycorrhizal symbiont
Tylopilus felleus (Bull.: Fr.) Karst.	*Boletus felleus* Bull.: Fr.	mycorrhizal symbiont
Tympanis pinastri (Pers.: Fr.) Tul.		bark saprophyte
Tyromyces amarus (Hedgc.) Lowe	*Polyporus amarus* Hedgc.	pocket dry rot

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Tyromyces balsameus (Pk.) Murr.	*Polyporus balsameus* Pk. (See also *Climacocystis*)	brown cubical rot
Tyromyces borealis (Fr.) Imaz.	*Polyporus borealis* Fr.	heart rot
Tyromyces spraguei (Berk. et Curt.) Murr.	*Polyporus spraguei* Berk. et Curt.	root rot
Uncinula circinata Cke. et Pk.		powdery mildew
Uncinula clintonii Pk.		powdery mildew
Uncinula flexuosa Pk.		powdery mildew
Uncinula salicis Wint.		powdery mildew
Uredinopsis pteridis Diet. et Holw. in Diet.	*Uredinopsis macrosperma* Cke.	needle rust
Uredinopsis struthiopteridis Stormer		needle rust
Uromyces digitatus Wint.		koa leaf blister
Uromyces koae Arth.		koa witches' broom
Ustulina vulgaris Tul.		wood rot
Ustulina deusta (Hoff.: Fr.) Lind.		trunk rot
Valsa kunzei Fr.		canker
Venturia acerina Plak.		leaf spot
Venturia macularis (Fr.) Mull. et v. Arx	*Venturia tremulae* Aderh.	shepherd's crook shoot blight
Venturia populina (Vuill.) Fabrici		shepherd's crook shoot blight
Verticicladiella wageneri Kend.	*Ceratocystis wageneri* Goheen et Cobb (Perfect state)	black stain root rot
Verticillium albo-atrum Reinke et Berth.		Verticillium wilt
Virgella robusta (Tub.) Darker		needle cast
Virus - Cucumber mosaic		cucumber mosaic virus
Virus - Maclura mosaic		Maclura mosaic virus
Virus - *Morsus ulmi*		elm phloem necrosis virus
Wolfiporia cocos (Wolf) Ryv. et Gilbn.	*Poria cocos* Wolf	brown root and butt rot
Xiphinema americanum Cobb		dagger nematode
Xylobolus frustulatus (Pers.: Fr.) Boidin		white pocket rots of hardwoods

Checklist of Birds

Common name	Scientific name[1]
Bananaquit	*Coereba flaveola*
Bluebird, Mountain	*Sialia currucoides*
Bobwhite, Northern	*Colinus virginianus*
Cardinal	*Cardinalis cardinalis*
Chachalaca, Plain	*Ortalis vetula*
Chickadee, Black-capped	*Parus atricapillus*
Crossbill,	
Red	*Lorix curvirostra*
White-winged	*Lorix leucoptra*
Crow	*Corvus* spp.
Fish	*Corvus ossifragus*
Dove, Mourning	*Zenaida macroura*
Duck, Wood	*Aix sponsa*
Eagle,	
Bald	*Haliaeetus leucocephalus*
Golden	*Aquila chrysaetos*
Egret, Great	*Casmerodius albus*
Finch, Purple	*Carpodacus purpureus*
Flicker, Northern	*Colaptes auratus*
Goldeneye, Common	*Bucephala clangula*
Goldfinch, American	*Carduelis tristis*
Grackle, Common	*Quiscalus quiscula*
Grosbeak,	
Evening	*Coccothraustes vespertinus*
Pine	*Pinicola enucleator*
Rose-breasted	*Pheucticus ludovicianus*
Grouse,	
Blue	*Dendragapus obscurus*
Spruce or Franklin's	*Dendragapus canadensis*
Ruffed	*Bonasa umbellus*
Sharp-tailed	*Tympanuchus phasianellus*
Gull, Ring-billed	*Larus delawarensis*
Hawk, Red-tailed	*Buteo jamaicensis*
Jay,	
Blue	*Cyanocitta cristata*
Pinyon	*Gymnorhinus cycanocephalus*
Scrub	*Aphelocoma coerulescens*
Steller's	*Cyanocitta stelleri*
Junco, Dark-eyed	*Junco hyemalis*
Kinglet,	
Golden-crowned	*Regulus satrapa*
Ruby-crowned	*Regulus calendula*
Mallard	*Anas platyrhynchos*
Mockingbird, Northern	*Mimus polyglottus*
Nutcracker, Clark's	*Nucifraga columbiana*
Nuthatch,	
Brown-headed	*Sitta pusilla*
Red-breasted	*Sitta canadensis*
White-breasted	*Sitta carolinensis*
Osprey, American	*Pandion haliaetus*
Ovenbird	*Seiurus aurocapillus*
Owl, Great Gray	*Strix nebulos*
Parakeet, Carolina	extinct
Parrot, Puerto Rican	*Amazona vittata*

Common name	Scientific name[1]
Partridge, Hungarian	*Perdix perdix*
Parula, Northern	*Parula americana*
Pheasant, Ring-necked	*Phasianus colchicus*
Pigeon	*Columba* spp.
Band-tailed	*Columba gasciata*
Prairie-chicken, Greater	*Tympanuchus cupido*
Quail, California	*Callipepla californica*
Redpoll, Common	*Carduelis flammea*
Reina Mora	*Spindalis zena*
Robin, American	*Turdus migratorius*
Sapsucker,	
Red-breasted	*Sphyrapicus ruber*
Williamson's	*Sphyrapicus thyroideus*
Yellow-bellied	*Sphyrapicus varius*
Siskin, Pine	*Carduelis pinus*
Sparrow,	
Black-throated	*Amphispiza bilineata*
Song	*Melospiza melodia*
White-throated	*Zonotrichia albicollis*
Starling, European	*Sturnus vulgaris*
Tanager, Striped-headed	*Spindalis zena*
Thrasher, Pearly-eyed	*Margarops suscatus*
Thrush,	
Red-legged	*Turdus blumbea*
Varied	*Ixoreus narvius*
Turkey, Wild	*Meleagris gallopavo*
Veery	*Cathatus fuscescens*
Warbler,	
Bachman's	*Vermivora bachmanii*
Black-and-white	*Mniotilta varia*
Blackburnian	*Dendroica fusca*
Black-throated Green	*Dendroica virens*
Cape May	*Dendroica tigrina*
Kirtland's	*Dendroica kirtlandii*
Magnolia	*Dendroica magnolia*
Nashville	*Vermivora ruficapilla*
Pine	*Dendroica pinus*
Prothonotary	*Protonotaria citrea*
Yellow-throated	*Dendroica dominica*
Waxwing,	*Bombycilla* spp.
Bohemian	*Bombycilla garrulus*
Cedar	*Bombycilla cedrorum*
Woodcock, American	*Scolopax minor*
Woodpecker,	
Acorn	*Melanerpes formicivorus*
Downy	*Picoides pubescens*
Hairy	*Picoides villosus*
Pileated	*Dryocopus pileatus*
Red-bellied	*Melanerpes carolinus*
Red-cockaded	*Picoides borealis*
Red-headed	*Melanerpes erythrocephalus*
White-headed	*Picoides albolarvatus*
Yellowthroat, Common	*Geothlypis trichas*

Checklist of Mammals

Common name	Scientific name
Agouti	*Dasyprocta* or *Myoprocta* spp.
Bat, Jamaican Fruit-eating	*Artibus jamaicensis*
Bear,	
Black	*Ursus americanus*
Grizzly	*Ursus arctos*
Beaver,	
American	*Castor canadensis*
Mountain	*Aplodontia rufa*
Bighorn Sheep	*Ovis canadensis*
Bison	*Bison bison*
Caribou (Woodland)	*Rangifer tarandus*
Chickaree (Red Squirrel)	*Tamiasciurus* spp.
Chipmunk	*Tamias* spp.
Cliff	*Tamias dorsalis*
Eastern	*Tamias striatus*
Least or Western	*Tamias minimus*
Cottontail (American Rabbit)	*Sylvilagus* spp.
Desert	*Sylvilagus audubonii*
Eastern	*Sylvilagus floridanus*
Mountain	*Sylvilagus nuttallii*
New England	*Sylvilagus transitionalis*
Coyote	*Canis latrans*
Deer,	
Black-tailed or Mule	*Odocoileus hemionus*
White-tailed	*Odocoileus virginianus*
Elk (Wapiti)	*Cervus elaphus*
Roosevelt	*Cervus elaphus roosevelt*
Fox,	
Gray	*Urocyon cinereoargenteus*
Red	*Vulpes vulpes*
Ground Squirrel,	
Golden-mantled	*Spermophilus lateralis*
Thirteen-lined	*Spermophilus tridecemlineatus*
California or Beechey's	*Spermophilus beecheyi*
Hare	*Lepus* spp.
Snowshoe	*Lepus americanus*
Jack Rabbit	*Lepus* spp.
Lynx, Canadian	*Lynx canadensis*
Marmot, Hoary	*Marmota caligata*
Marten, Pine	*Martes americana*
Mice, Meadow (Voles)	*Microtus* spp.
Moose	*Alces alces*
Mountain Goat	*Oreamnos americanus*
Mouse,	
California	*Peromyscus californicus*
Deer	*Peromyscus maniculatus*
Pinyon	*Peromyscus truei*
White-footed	*Peromyscus leucopus*
Nutria	*Myocastor coypus*
Opossum, Virginia	*Didelphis virginiana*
Peccary	*Tayassu* spp.
Pika	*Ochotona princeps*
Pocket Gopher,	
Eastern	*Geomys* spp.
Western	*Thomomys* spp.
Porcupine	*Erethizon dorsatum*
Rabbit (American)	*Sylvilagus* spp.
Brush	*Sylvilagus bachmani*
Swamp	*Sylvilagus aquaticus*
Raccoon	*Procyon lotor*
Rat (Old World)	*Rattus* spp.
Polynesian	*Rattus exulans*
Tree	*Rattus rattus*
Shrew (Red-toothed)	*Sorex* spp.
Skunk	*Conepatus* spp.
Squirrel (Flying)	*Glaucomys* spp.
Squirrel (Red)	*Tamiasciurus* spp.
Douglas'	*Tamiasciurus douglasii*
Pine, Red, or Spruce	*Tamiasciurus hudsonicus*
Squirrel (Tree)	*Sciurus* spp.
Abert's (Kaibab)	*Sciurus aberti*
Eastern Fox	*Sciurus niger*
Eastern Gray	*Sciurus carolinensis*
Western Gray	*Sciurus griseus*
Vole (Meadow)	*Microtus* spp.
Creeping or Oregon	*Microtus oregoni*
Montane	*Microtus montanus*
Vole (Pine)	*Pitymys* spp.
Pine or Woodland	*Pitymys pinetorum*
Vole (Red-backed)	*Clethrionomys* spp.
Gapper's Red-backed	*Clethrionomys gapperi*
Wild Pig	*Sus scrofa*
Wolf, Gray or Timber	*Canis lupus*
Wolverine	*Gulo gulo*
Woodchuck	*Marmota monax*
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